Library 145 MAY 8 1939

Vol. 66 MAY, 1939 No. 5

Bulletin

of the

Torrey Botanical Club

Editor
R. P. Wodehouse

Associate Editors

Irving W. Bailey
Edward W. Berry
M. A. Chrysler
Bernard O. Dodge
Henry Allan Gleason
Tracy Elliot Hazen
Michael Levine
William J. Robbins
George M. Reed
John W. Shive

CONTENTS

Spore Production in Regnellidium ....*M. A. Chrysler and D. S. Johnson* 263

Studies on Rhizophidium. III. Germination of the Resting Spores ....*J. S. Karling* 281

Flower Buds and Phylogeny of Dicotyledons .....*Alfred Gundersen* 287

Lagenospermum imparirameum sp. nov., a Seedbearing Fructification from the Mississippian of Pennsylvania and Virginia ....*Chester A. Arnold* 297

Notes on the Botanical Components of Curare—II ....*B. A. Krukoff and A. C. Smith* 305

The Morphology and Phylogenetic Position of the Genus Jouvea (Gramineae) .....*Paul Weatherwax* 315

The Taxonomy and Ecology of Agropyron spicatum and A. inerme .. ..*Rexford F. Daubenmire* 327

Index to American Botanical Literature 330

Published for the Club monthly except
July, August, and September
by
GEORGE BANTA PUBLISHING COMPANY, MENASHA, WISCONSIN
Subscription price $6.00 per year

Entered as Second Class Matter at the Post Office at Menasha, Wisconsin
Accepted for mailing at special rate of postage provided for in the act of February 28, 1925, embodied in paragraph 4, section 412, P. L. and R., authorized July 23, 1928.

THE TORREY BOTANICAL CLUB

President
ARTHUR H. GRAVES, PH.D.
Brooklyn Botanic Garden, Brooklyn, New York

Vice-Presidents
GEORGE T. HASTINGS, M.A.
CORNELIA L. CAREY, PH.D.

Corresponding Secretary
J. S. KARLING, PH.D.
Columbia University, New York City

Recording Secretary
MISS FLORENCE CLYDE CHANDLER, A.M.

Treasurer
HAROLD N. MOLDENKE, PH.D.
The New York Botanical Garden, Bronx Park, New York

Editor
R. P. WODEHOUSE, PH.D.

Bibliographer
MRS. MARGUERITE B. FULLING

Business Manager
MICHAEL LEVINE, PH.D.

MEETINGS

Meetings twice each month from October to May, inclusive: the first Tuesday at 8:15 P.M., at the American Museum of Natural History or at Columbia University; the third Wednesday at 3:30 P.M., in the Museum Building of the New York Botanical Garden, Bronx Park, New York, N.Y.

PUBLICATIONS

All subscriptions and other business communications relating to the publications of the Club should be addressed to the Treasurer, Dr. H. N. Moldenke (mail address, New York Botanical Garden, Bronx Park, New York, N.Y.). Matters relating to advertisements and circulation should be referred to Dr. Michael Levine, Montefiore Hospital, New York, N.Y. All communications regarding exchanges should be referred to the Corresponding Secretary, who is Chairman of the Exchange Committee on Publications.

Bulletin. Established 1870. Monthly, except during July, August, and September. Price, $6.00 a year; single numbers 75 cents. Of former volumes, only 24-56 can be supplied separately; certain numbers of other volumes are available, but the entire stock of some numbers has been reserved for the completion of sets. Manuscripts intended for publication in the BULLETIN should be addressed to Dr. R. P. Wodehouse, 75 Ridge Drive, Yonkers, N.Y. The editors may accept papers up to 20 pages in length, with illustrations and tabular matter generally not exceeding twenty per cent of that amount. Longer and more copiously illustrated papers, however, may be published if the excess pages, illustrations, and tabular matter are paid for by the contributors. Claims for missing numbers should be made to the Treasurer within 60 days following their date of mailing. The Treasurer will supply missing numbers free only when they have been lost in the mails.

Torreya. Bimonthly, established 1901. Price, $1.00 a year. Manuscripts intended for publication in TORREYA should be addressed to Mr. George T. Hastings, Editor, 2587 Sedgwick Ave., New York, N.Y.

Memoirs. Occasional, established 1889.

Preliminary Catalogue of Anthophyta and Pteridophyta within 100 miles of New York City, 1888. Price, $1.00.

Reprints. Contributors of articles accepted for publication in the BULLETIN should order reprints, if desired, when they return galley proofs to the editor. They may be ordered through the editor from the George Banta Publishing Company, the contributor paying for all his reprints. A schedule of rates is sent with galley proof.

BULLETIN
OF THE
TORREY BOTANICAL CLUB

VOLUME 66 MAY · 1939 NUMBER 5

Spore Production in Regnellidium

M. A. CHRYSLER AND D. S. JOHNSON[1]

(WITH PLATE 5 AND FIFTEEN FIGURES)

The paper by Johnson and Chrysler (1938) dealt with the structure and development of the stem, root, leaf and sporocarp of *Regnellidium diphyllum*. Although this Brazilian plant was discovered by Lindman in 1892, and recognized by him as a new genus of Marsileaceae (Lindman, 1904), only a habit study could be undertaken until properly preserved material was available. The material used in the present instance is the same as in the previous paper, and was fixed in the field through the cooperation of Doctor Rau and Doctor Dutra, whose services have made the present studies possible. Several stains were employed: Delafield's haematoxylin for younger stages, safranin and fast green for ripe spores, iron alum haematoxylin, also the tannic acid-ferric chloride combination proposed by Foster (1934). The last method was found to be especially useful in improving the definition of thin cell walls. Sporocarps of *Marsilea* have been available for comparison, through the kindness of Professor W. E. Manning of Smith College.

DEVELOPMENT OF THE SPORANGIA

The origin of the soral initials, development of the soral ridges arising from these, and submergence of these by overgrowth of surrounding tissues of the young sporocarp, have been described and figured in the previous paper (1938). At the stage shown in figure 52 of the paper just mentioned, each soral receptacle is situated on the side of a narrow cavity

[1] Botanical contribution from the Johns Hopkins University, No. 150.

Most of the slides used in this study and a number of helpful notes concerning them were prepared by the late Doctor Duncan S. Johnson and were made available through Mrs. Johnson after his death on February 16, 1937. The present contribution constitutes a continuation of the study projected by Doctor Johnson.—M.A.C.

[THE BULLETIN FOR APRIL (66: 193–261) WAS ISSUED APRIL 5, 1939]

opening to the exterior by a small ventral pore. A series of superficial cells of each receptacle are found to be larger than their neighbors, and each becomes divided by an oblique wall which at its lower edge reaches the base of the superficial cell (fig. 1). Next, another oblique wall, opposite the first, appears, and the apical cell of a megasporangium is established. At a slightly later date the same receptacle gives rise to microsporangia. In figure 32 of Johnson's paper of 1898 is shown a slightly developed acropetal succession in the sporangia on a receptacle, that is, a few of the sporangia nearest the ventral end of the sorus are later in beginning their development. We find also in *Regnellidium* that a group of younger sporangia occur at the ventral end, as determined by an inspection of the sporocytes and also of the tapetum. Thus, in figure 37 the sporangium nearest the dorsal end of the receptacle has sporocytes at metaphase of the first meiotic division, while the tapetum has broken up into the plasmodium; the sporangium at the ventral extremity shows sporocytes recently formed, with tapetum still intact; the two sporangia lying midway have sporocytes in early stages of meiosis. Since in *Regnellidium* the vascular supply enters the receptacle at its dorsal end (fig. 16), there may be significance in this tendency to an acropetal sequence of sporangia. The arrangement of sporangia on the soral receptacle is complicated by the width of the latter and by its raised position above the partition upon which it arises. The rather liberal size of the soral canals, due in turn to the shape of the capsule, and the relatively small number of canals also appear to allow room for the sori to spread, so that the megasporangia come to occupy more than the single row which is characteristic of *Marsilea*, while the microsporangia sit not only along the edges of the receptacle but are also found among the megasporangia (fig. 17). Since the sporangia are of various ages, the arrangement should be regarded as a modification of the gradate condition, tending toward the mixed.

We shall trace first the development of a microsporangium, for this is particularly clear on account of the longer stalk. Stages are shown in figures 2–10, in which it may be seen that about six cells are cut off right and left from the apical cell before the cap cell is formed. Because of the finding by Johnson (1898, p. 136) of a tetrahedral apical cell in the microsporangium of *Marsilea*, it is important to establish the shape of the cell in *Regnellidium*. With figures 4 and 7–10 should be compared figures 2 and 3 which we take to be views at right angles to the previous ones. Figure 5 represents a section taken nearly transverse to the tip of a sporangium. These appear clearly to represent respectively the end, side and top views of a dolabriform (or "zweischneidig") apical cell. One other section is significant; figure 6 shows a transverse cut through a sporangium stalk. A;

"zweischneidig" but not a tetrahedral apical cell could produce a stalk having four rows of cells. From figure 2 it will be noticed that promptly after a segment is cut off from the apical cell a longitudinal anticlinal division occurs; in this way the stalk comes to have four rows of cells. We may then regard as proven that the apical cell belongs to the dolabriform type. It should be added that transverse sections through tips of sporangia have failed to show examples of a triangular cell such as is frequently figured as characteristic of the apical cell in Polypodiaceae. The possibility of occurrence of tetrahedral cells is not denied; moreover it may be that an apical cell can begin dolabriform and later become tetrahedral. There is no constancy in orientation of the sporangia; of the members of a row, some show the end of the wedge-shaped initial, while others present one of the more or less flat faces, e.g., the group of three sporangia shown in figures 2, 3 and 4. In spite of their stalk the microsporangia scarcely reach the level of the top of the rapidly growing megasporangia. The latter (fig. 11) are early to be distinguished by their broad short stalk, a condition brought about by growth in width and also division of the stalk cells.

Tapetum.—After cutting off the cap-cell, the apical cell becomes the archesporial cell; two anticlinal walls are formed in succession, then a periclinal wall (figs. 11, 12). The cells cut off externally by these form what may be called the primary tapetal cells; they divide by anticlinal walls (as does also the cap cell), then by periclinal walls cutting off an external layer of flat cells and leaving an inner layer of cuboidal cells (figs. 14, 18). The flat cells of the outer layer show no more cytoplasm than do the so-called jacket cells which make up the wall of the sporangium, but the cuboidal cells stain rather deeply and have a prominent nucleus. These cells divide actively by mitosis in all three planes to form a true tapetum two to three or even four cells in thickness (fig. 19). The number of layers of cells varies in different parts of a sporangium, being greater in places where a slight cavity is left by the rounding off of the contiguous sporocytes. The tapetal cells do not enlarge, as they do in many plants, but increase the bulk of nutritive material by division. Their width is about 85μ, and their walls are extremely thin, so that boundaries of some of the cells are hard to distinguish, but the nuclei are arranged in rather regular radial rows (fig. 19) and some of the cells may be binucleate through solution of walls. Shortly prior to separation of the sporocytes the walls of the tapetum break down, and the comparatively regular arrangement of the nuclei disappears (fig. 20). The flat cells previously described (see figs. 14, 18–21), however, retain their shape and contents, and appear to function as part of the sporangium wall. Immediately following this phase, alveoli

or vacuoles begin to appear in the outer part of the true tapetum (fig. 20), and at first have a diameter somewhat less than that of tapetal cells. Formation of alveoli spreads to the central part of the tapetal mass, which must now be called a periplasmodium. The boundaries of the vacuoles become so distinct that the mass simulates a tissue (fig. 25), although it may be readily distinguished by its foam structure and an increasing difference in size of the meshes. In the meshes of this vacuolate mass lie the nuclei, in which no further divisions have been seen to occur. The vacuoles of the outer region of the plasmodium increase considerably in size, while the region next the tetrads shows only small vacuoles and few nuclei. The latter begin to accumulate around the now separating members of the tetrads, and the plasmodium invades the intervening spaces (figs. 21, 22), bringing about a dispersal of the tetrads through the sporangial cavity. The activity of the plasmodium in building up the epispore will be considered later.

DEVELOPMENT OF THE MEGASPORES

While the tapetum has undergone the transformation into periplasmodium, the sporogenous region has kept pace. Starting with the primary sporogenous cell left after the primary tapetal cells have been cut off, this cell typically appears to undergo four ordinary divisions resulting in the production of sixteen sporocytes. The frequency of sporangia having an ellipsoidal form with the long axis parallel with that of the receptacle is noticeable. In such sporangia the group of sporocytes consists of four rows of four cells each, the long axis of this group again being parallel to the surface of the receptacle. Miss Marschall (1925) figures the same condition for *Marsilea*. In some cases one or more of the divisions fails to occur; for instance in figure 15 is shown a sporangium in which only thirteen sporocytes are found by a study of serial sections.

Even before the sporocytes round off, and while the tapetum is passing into the alveolar condition, the early phases of meiosis are to be seen. Although the preservation of our material leaves much to be desired for cytological work, the following stages have been observed: leptonema, synizesis (!) diakinesis, metaphase, anaphase and telophase of division I, metaphase and telophase of division II. Especially in the diakensis stage it may be noticed that one pair of chromosomes is definitely longer than any of the others (fig. 36). Miss Marschall (1925) has called attention to this feature of the sporocytes in *Marsilea*, although no figure is provided. The presence of satellites in another chromosome pair is to be seen in figure 36. × and + forms of chiasma are frequent. In a few cases of diakinesis it was possible to make chromosome counts, and from these we tentatively estimate $n = 16$. Mitotic figures are plentiful in developing

sporangia, but faulty fixation has resulted in clumping, so that determination of 2n has been impracticable.

As the members of a tetrad separate they are seen to be tetrahedral with the usual triradiate ridges which are retained more or less permanently by the microspores. The potential megaspores however round off, especially one of them in one of the tetrads; this spore increases in size while the other three remain undeveloped although still closely associated with the functional one. This stage was observed only a few times (fig. 23). As yet the wall of the megaspore is very thin and the spore is spherical. The plasmodium has already been described as surrounding each tetrad, with a more or less homogeneous layer next the spores. The tapetal nuclei now appear to cluster around the functional member of the tetrad, leaving the outer part of the plasmodium rather coarsely alveolar (fig. 25). The functional spore now becomes placed near the middle of the sporangium, and the spore-wall increases in thickness, thus beginning the formation of the epispore. At the region where the three non-functional spores lie in contact with the developing one, growth of the megaspore-wall is checked (fig. 24), resulting eventually in production of the curious "papilla." Shrunken remains of one or more of the three abortive members of the tetrad are frequently to be seen at this location, lying in a cup-shaped cavity of the megaspore-wall after this has attained a thickness of 7μ (fig. 24). At this stage the wall gives no hint of the complexity soon to be attained. During these early stages the cytoplasm of the megaspore is scanty, forming a thin lining inside the wall: the nucleus is hard to find, although later it may readily be seen in its final position directly under the thin part of the wall, lying in cytoplasm practically free from starch, although oil globules are present. Ellipsoid starch grains averaging 55 × 37 appear in the peripheral part of the spore cavity (fig. 29), and increase in numbers as the spore ripens until the whole cavity is filled with the mixture of starch grains and oil globules, imbedded in a small amount of cytoplasm (fig. 33).

Meanwhile much of the material of the plasmodium and abortive spores has been consumed in increasing the thickness of the epispore and in developing the characteristic structure which distinguishes this wall layer. For a considerable period the plasmodial nuclei lie clustered more or less unevenly around the thickening megaspore wall—as many as fifty of them can be counted in a single section, and they present every appearance of being active factors in the important metabolic and structural changes which are going on, but eventually they disappear (no stages have been available for study of this process) and the alveolar region of the plasmodium is converted into wall material. At a late date also occurs the dissolution of the outermost, flat-celled layer of tapetum.

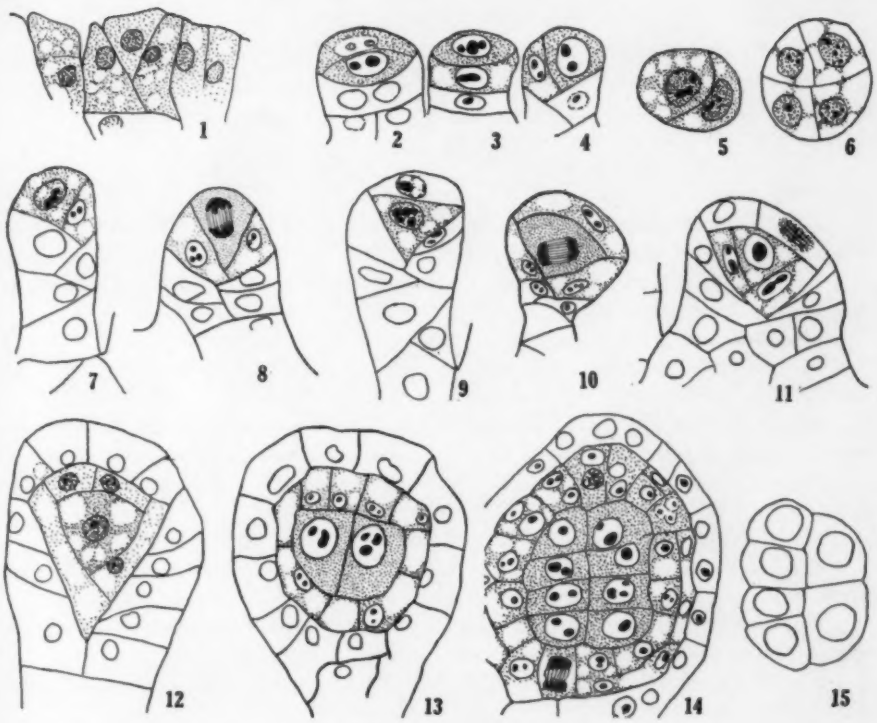
Although normally a single megaspore develops in a sporangium, cases have been observed where two cells of a tetrad develop at least part way into spores. Such a case is represented in figure 26. Another case has been found where three of the members of a tetrad exhibit early stages in differentiation (fig. 27). In another instance two tetrads appear to have begun formation of a megaspore apiece (fig. 28). As many as three sporocytes may begin development and the megaspores may reach a diameter of 50μ. Russow (1872) makes the following reference to *Marsilea:* "in a few cases three vesicles (Blasen) were visible, yet in all cases only one of them developed further." Similar stages were found in *Marsilea* by Shattuck (1910), who regarded them as indicating "sharp rivalry between two or more enlarging potential megaspores." In *Regnellidium*, as in *Marsilea*, "in the end, one centrally placed spore always gains the ascendancy, the others becoming abortive." We have observed that these multiple spores are apt to occur in soral chambers at one end of a sporocarp, suggesting that nutrition may be a factor.

THE MEGASPORE WALL

The mature spore (actually a sporangium, as will be seen later) has a diameter of 0.6 mm, is approximately spherical, creamy white, and finely roughened so as to have a rather dull surface. At one point is a round spot 0.2 mm in diameter, slightly lighter in color, and generally raised into a short nipple-shaped process, the so-called papilla, which represents the thin place in the wall where the three abortive members of the tretrad were situated. When one of these "spores" is placed in a drop of water, an outer membrane is quickly ruptured, and a mucilaginous mass exudes, rapidly swelling due to absorption of water, and surrounding the spore proper. The membrane just mentioned consists of a layer of flat cells, the walls of which consist largely of cellulose, as determined by application of iodine followed by sulphuric acid; it is the wall of the sporangium.

Figure 29 represents a section through a nearly ripe spore, prepared by the paraffin method and therefore showing none of the mucilaginous coating and only fragments of the sporangium wall. At the upper end is to be seen the "papilla," consisting entirely of epispore. Beneath the primary spore-wall lies the ovoidal nucleus imbedded in cytoplasm containing oil globules, but nearly free from starch grains, as previously mentioned. These however form a peripheral layer elsewhere in the spore, and eventually fill the whole cavity. Figure 30 represents a section through the wall of a ripe spore, and in it four layers can readily be distinguished:

1. *Endospore*, the primary cell-wall lying next the cytoplasm. Its thickness is about 3.2μ, and it is continuous under the papilla, where it bulges,



Figs. 1–15: stages in development of sporangia, all ×445.

Fig. 1. Long. sec. through superficial region of a soral ridge. One of the cells has been divided by two oblique walls, forming the apical cell of a sporangium.

Figs. 2–4. Groups of microsporangia, side view, from preparation similar to fig. 17. In fig. 4 the dolabriform apical cell lies in a position at right angles to that of fig. 2 and 3.

Fig. 5. Dolabriform apical cell of microsporangium viewed from above.

Fig. 6. Trans. sec. through stalk of a microsporangium.

Fig. 7. Older microsporangium.

Fig. 8. Sporangium cutting off cap cell.

Fig. 9. Sporangium with archesporial cell.

Fig. 10. Sporangium with archesporial cell dividing to cut off first tapetal cell.

Fig. 11. Megasporangium. Two tapetal cells cut off.

Fig. 12. Tapetal cells cut off, leaving primary sporogenous cell.

Fig. 13. Early stage in division of primary sporogenous cell; tapetum still a single layer.

Fig. 14. Sporocytes in middle, followed by tapetum in which one cell is dividing to form a flat cell of the outer layer and a larger cell of the inner tapetal layer.

Fig. 15. Group of sporocytes, being those lying in one plane out of a set of thirteen. See fig. 17.

Explanation of Plate 5

Figs. 16–30 and 33–37, *Regnellidium*, 31 and 32, *Marsilea*

Fig. 16. Trans. sec. through developing sporocarp, showing two of the soral canals each containing a soral receptacle with its vascular supply. At the lower edge of the figure one of the ventral pores has nearly closed. ×30.

Fig. 17. Portion of a soral receptacle, showing microsporangia among the megasporangia. ×95.

Fig. 18. Sporangium about the age of the one in fig. 13, with differentiation between inner and outer tapetal layers. ×415.

Fig. 19. Sporangium with sporocytes and a tapetum composed of outer layer of flat cells and inner layer which has divided to be about three cells thick. ×350.

Fig. 20. Slightly older sporangium with sporocytes in diakinesis. The walls of the tapetum have broken down and the alveolar plasmodium has replaced the tapetum. ×330.

Fig. 21. End of the second meiotic division. Tapetal nuclei are less numerous in the outer part of plasmodium. ×330.

Fig. 22. Spores are now separated, and plasmodial nuclei have invaded the central area. ×420.

Fig. 23. One spore has begun to enlarge, others are disintegrating. ×390.

Fig. 24. Megaspore has enlarged and wall has thickened except at one place where remains of the tetrad may be seen. Abortive spores lie above these. ×295.

Fig. 25. Older megaspore with tapetal nuclei clustered around it, also the very coarse meshes of the plasmodium. ×260.

Fig. 26. Abnormal tetrad in which two members have partly developed into megaspores. The uneven distribution of the plasmodial nuclei is typical. ×375.

Fig. 27. A case similar to fig. 26; here three members of a tetrad have undergone some development. ×375.

Fig. 28. Attempt of two tetrads to function in a sporangium. ×270.

Fig. 29. Long. sec. through a nearly mature megaspore. The nucleus is visible below the apical papilla. A thin layer of starch grains lies against the primary wall of the spore. ×75.

Fig. 30. Sec. through wall of the megaspore shown in fig. 29. The layer of starch grains is followed by a thin layer of cytoplasm (black), next by the endospore (gray), inner layer of epispore (black), prismatic layer, outer or papillar layer. ×270.

Fig. 31. Sec. of wall of megaspore of *Marsilea quadrifolia* for comparison. Poor development of the papillar layer is to be noted. At the right is a portion of the mucilaginous layer. ×270.

Fig. 32. Tangential sec. through prismatic layer of *Marsilea*, showing the interprismatic substance. ×330.

Fig. 33. Apical region of mature megaspore. The cavity of the spore is now filled with starch and oil, and the nucleus lies beneath a slight bulge in the primary wall outside which lies the papilla. The inner epispore stops at the edge of the papilla, but the prismatic layer bends outward to form the papilla. Covering these is the outer layer of epispore, ragged above the papilla. ×130.

Fig. 34. Microspores, with one tetrad surrounded by a common prismatic layer. ×165.

Fig. 35. Older microspores, showing two cases where a prismatic layer surrounds more than one spore, also a prismatic layer surrounding two tetrads. ×160.

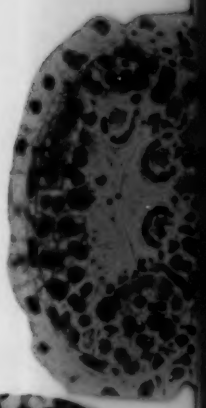
Fig. 36. Chromosome pairs visible at one plane of a sporocyte in diakinesis. One large pair occurs at the left. ×1800.

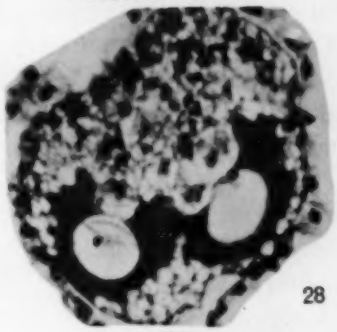
Fig. 37. Long. sec. through a sorus, showing acropetal succession in megasporangia. See text. ×80.

16

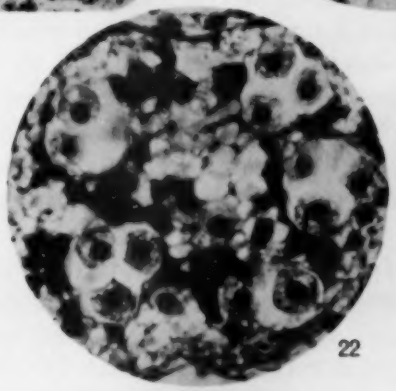
17

18

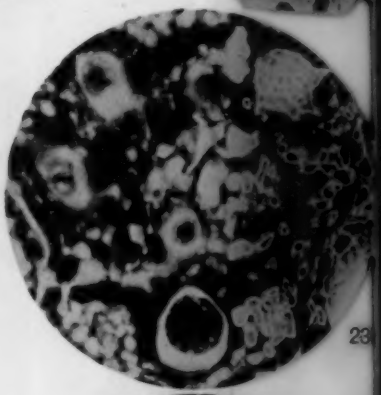




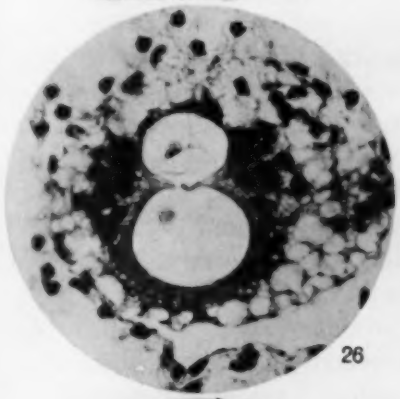
28



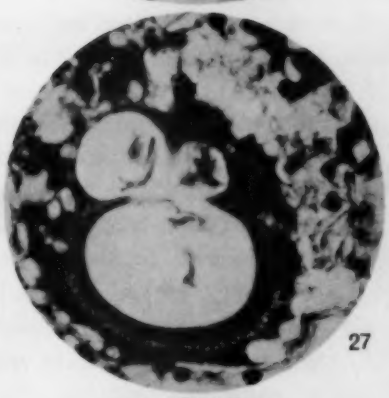
22



23

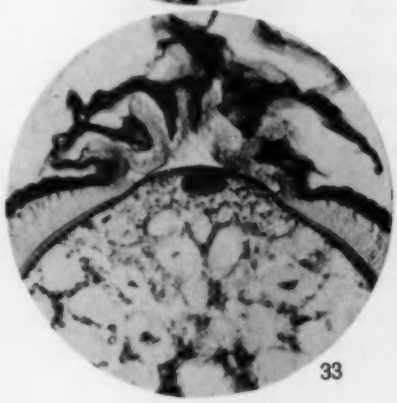


26



27

29



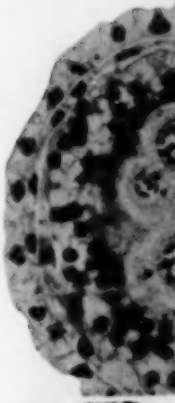
33

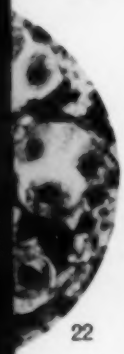
34

35

18

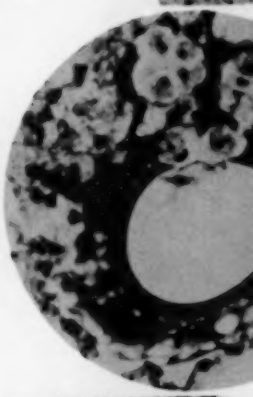
19

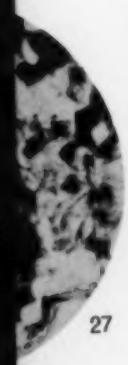




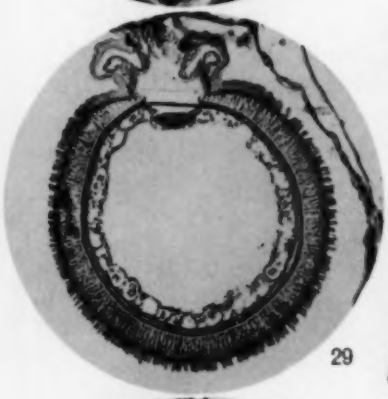
22

23

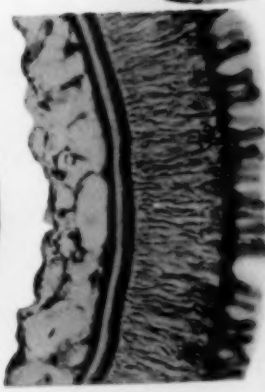


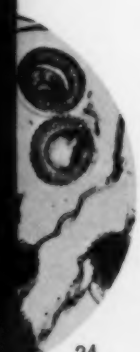


27



29



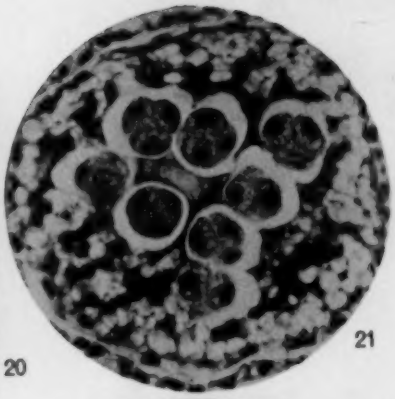


34

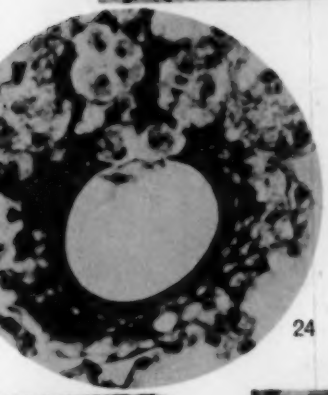
35

CHRYSLER: REGNELLIDIUM

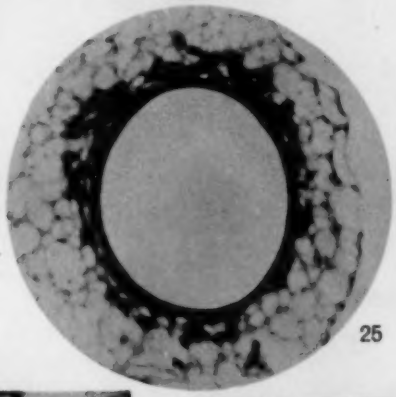
20



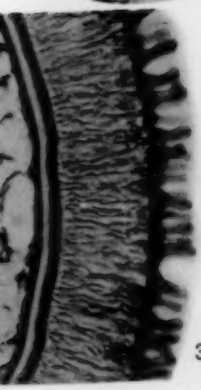
21



24

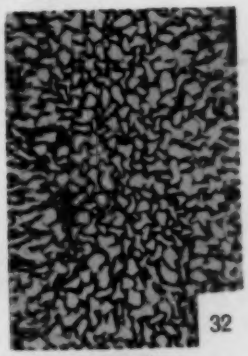


25

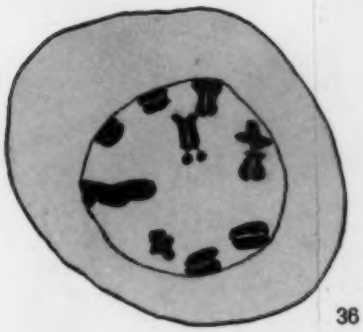


30

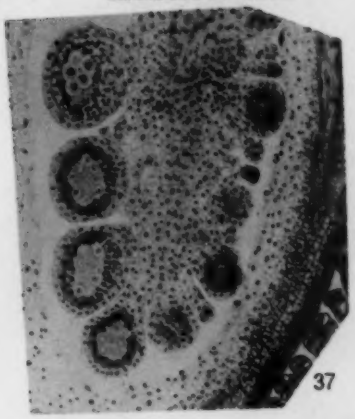
31



32



36



37

UNIV. OF MICH.

as is seen in the photograph of this region of a ripe spore (fig. 33). Meunier (1888) says that in *Pilularia* this layer consists of almost pure suberin.

2. *Inner layer of epispore* (called by some authors exospore, perispore, perineum; we prefer the first term on account of its drawing attention to the fact that it is laid down externally, namely by the action of the plasmodium). It has a thickness of about 4μ, is closely applied to the endospore, and appears homogeneous. At the edge of the papilla it comes to a stop—the papilla consists of layer 3 alone. It gives no reaction for either cellulose or lignin; left for several hours in solution of chromic acid it dissolves; it stains reddish with sudan IV. These reactions indicate suberin, in spite of no appearance of a high degree of refractive power. The presence of cellulose or other substances may be masked (a useful discussion of this possibility in the case of meristems occurs in Tupper-Carey and Priestley, 1923). This layer may be regarded as a sort of foundation for the next to be described.

3. *Prismatic layer of epispore.* This forms the bulk of the wall, having a thickness of ca 45μ. It presents the appearance of radiating, slightly wavy lines uniting at the external surface of the layer. A section taken tangentially to the spore wall (fig. 32) shows that these wavy lines are really the walls enclosing more or less cylindrical narrow radiating spaces, the so-called prisms. Tangential sections of sufficient thickness show that the outer end of each prism is covered by a short conical cap formed by the inter-prismatic substance, so that the outer surface of the layer (as may be well seen where layer 4 is accidentally pulled away) presents a fine-papillar appearance, the units of which are about 4μ in height and breadth. Whether in the young spore-wall the prisms consisted of gas rather than some liquid or solid is to be doubted. The micro-chemical reactions correspond to those recorded for layer 2, so that the inter-prismatic substance must consist largely of suberin. This layer is continued into the wall of the papilla, where it has about the same structure but less than half the thickness; moreover it is irregularly wrinkled and lobed (not radially folded as in *Pilularia*), so that its full height is not manifest. There is nothing visible between the wall of the papilla and the endospore beneath.

4. *Papillate layer of epispore.* In the partly ripened spore shown in figure 30 this layer is conspicuous, for it stains with fast green and so contrasts strongly with the inner layers, which take a more or less deep stain with safranin. It is readily detachable from layer 3, and then appears as a series of papillae, each about 13.5μ high and 4μ wide, fitting over the ends of the low papillae which make up the surface of layer 3. As the spore ripens, the papillae of layer 4 seem to condense or shorten slightly, but the layer persists, and is distinguished by its reactions,

being insoluble in chromic acid, but responding positively to cellulose tests. At the edge of the papilla layer 4 separates from the prismatic layer, loses its papillate structure and forms a loose, thin membrane of ragged appearance.

Between the papillate layer and the sporangium wall lies a layer probably thicker than any of the others, consisting of a mucilaginous substance which absorbs water to a high degree. A corresponding layer exists in the other genera of the family, and Meunier (l.c.) considers that in *Pilularia* it constitutes the outermost layer of the spore wall. Whether this point of view is adopted for *Regnellidium* appears to us to be determined by the presence or absence of organization in the mucilaginous mass. Until structure of some sort can be demonstrated in the mass, we prefer to think of the papillate layer as the outermost part of the spore.

MICROSPORES

In the microsporangium the primary sporogenous cell undergoes the four successive divisions which have been found in the megasporangium. Each of the sixteen microsporocytes so formed may pass through the meiotic stages with production of four microspores. The total 64 are not always to be found, but generally 50 or more can be counted. The microspore has a diameter of about 40μ, that is, say one-fifteenth that of the megaspore. In shape (fig. 34) it is approximately spherical, but the "papilla" is larger in proportion than in the megaspore. Moreover the triradiate ridge persists more or less, the angle lying under the papilla. A short prickle is sometimes present, projecting into the papilla. The wall layers that can be made out with certainty are the endospore and the prismatic layer of the epispore. The latter has the same papillate pattern as in the megaspore, but the true outer papillate layer (numbered 4) is poorly developed. The thickness of the wall is ca. 10μ, of which the epispore constitutes say two-thirds. The nucleus occupies the same position as in the megaspore, namely, immediately under the papilla, but starch grains are absent. Thus the microspore is a small edition of the megaspore, but a trifle more clumsy in appearance.

Several cases have been observed where the prismatic layer surrounds a tetrad instead of an individual spore. Such a case is illustrated in figure 34. An older stage is represented in figure 35, showing several instances of two or more members of a tetrad lying loose in a layer of epispore. The largest of these probably represents the attempt of an epispore to surround two tetrads. These curious spores lay in one of the soral cavities situated at one end of a capsule, as was found in the case of the megasporangia mentioned earlier. Their occurrence lends support to the view that in the mega-

spore also the epispore is related to a whole tetrad. In *Marsilea*, Russow (1872) observed two, three or four microspores surrounded by a single epispore. Pollen grains more or less similar to these abnormal spores have been observed in *Cichorium* by Wodehouse (1929), who reports that the giant pollen grains are not functional. These observations lead Wodehouse to conclude that although the material of which the exine is composed comes from the tapetum, the power to organize this material into a normal exine resides in the protoplasm of the spore itself. Hence we meet the old question as to whether the plasmodium is made of living protoplasm.

DISCUSSION

Since the structure and development of all three genera of Marsileaceae are now fairly well known, we should be in a position to inquire into the relationships of the family. Of late years most students of the family have followed the lead of Campbell (1904) who proposed to ally Marsileaceae with Schizaeaceae. Bower (1926) has summed up the evidence, reaching the same conclusion. Eames (1936) has materially strengthened the case. Smith (1938) has recently dissented from this view, proposing to relate Marsileaceae with Cyatheaceae.

One of the criteria, order of development of the sporangia, is not well marked in Marsileaceae. On the basis of the appearance of the microsporangium initials on the sides of the receptacular ridge, following the appearance of the megasporangia on top of the ridge, the condition is considered to be gradate. We have called attention to another indication of the gradate condition, which was proposed by Campbell (1905), namely, the sporangia are slightly acropetal upon the soral ridge, with the youngest sporangia at the ventral end. This is especially well shown in *Regnellidium* because the vascular bundle enters the receptacle at its dorsal end (fig. 16, also Johnson and Chrysler, 1938) so that in this genus it is more appropriate to speak of the base and apex of the receptacle than in the case of *Marsilea*, where the vascular bundle enters near the middle. But the situation is complicated by the subsequent appearance of other sporangia among the older ones, so that there is plainly a tendency toward the mixed condition, as is well illustrated by *Regnellidium*. It is of interest to note that Stevens (1911) finds the sporangia of *Anemia* (Schizaeaceae) arise in acropetal succession. In Cyatheaceae the sporangia are reported as gradate, with transitions to mixed.

Concerning the shape of the apical cell of the sporangium, *Regnellidium* presents a dolabriform cell at least in its microsporangium, in contrast with the tetrahedral cell which Johnson (1898) reported for *Marsilea*. Since the leaf of *Marsilea* arises from a cell with two cutting faces (Han-

stein, 1865) and that of *Regnellidium* in the same way (Johnson and Chrysler, 1938), it is not surprising that in at least one genus of the family the sporangium should develop in like manner. The chief interest in the observation lies in the fact that two genera of Schizaeaceae, *Lygodium* and *Schizaea*, possess a dolabriform apical cell in their sporangia (Binford, 1907; Bartoo, 1929), while the Cyatheaceae are said to follow the rule for leptosporangiate ferns.

An unusually thick tapetum, originating from cells cut off from the archesporium, is characteristic of Marsileaceae and Salviniaceae (Kundt, 1911), also of Osmundaceae where however its origin is different. Attention should be drawn to the differentiation shown in the layers, the outermost one in *Regnellidium* being developed as flat, watery cells which persist as a jacket layer long after the inner, true tapetal cells have fused into the plasmodium. Miss Marschall (1925) reports the tapetum of *Marsilea* as consisting of two or three layers, while Meunier's (1888) beautiful figures of *Pilularia* show nothing thicker than a two-layered tapetum. Neither of these writers notes the persistence of the flat-celled layer. *Regnellidium* appears to exceed the other genera in thickness of the true tapetum, reaching three or locally even four layers in addition to the flat layer. The unusual development of the tapetum is no doubt connected with the great thickness of the megaspore wall, and this in turn appears to be specialized in connection with the aquatic habit, for we note a well-developed tapetum also in *Salvinia* (Kundt, 1911). Here however the layer is strictly a single one, with large cells which are for the most part binucleate. The tapetum in Cyatheaceae is stated to be of the regular two-layered type.

In view of the large number of divisions undergone by the tapetal cells of *Regnellidium*, the conspicuous assemblage of nuclei in the plasmodium is understandable. We do not find figures of any heterosporous pteridophyte in which the condition shown in figure 25 is reached. In *Pilularia* Meunier's figures indicate that the nuclei are not so numerous and undergo an earlier dissolution.

The development of a system of vacuoles through absorption of water appears to be related to the problems which arise in an aquatic plant, for Salviniaceae also show this feature.

The spore wall reaches a high degree of specialization in all genera of Marsileaceae. To a lesser extent the statement is true of the other heterosporous pteridophytes, while in the seed plants only the microspore wall is provided with the exine in which the special features are shown. No doubt the problems which are solved by the spores differ in the various groups. Probably one of the most common necessities is that of bringing the megaspore and microspore into close proximity, and it is usual to

"explain" along this line the common occurrence of spines. Such a device was worked out as early as the Carboniferous, witness the spiny exospore of *Bothrodendron* megaspores. Another Paleozoic plant, *Traquaria*, described by Williamson, and represented by sections deposited at the British Museum (Natural History), displays a remarkable exospore formed of interlacing filaments, the tips of which turn outward and render the spore prickly. There is even the appearance of a plasmodium. All of the heterosporous ferns are aquatics, so that the problems to be solved are

TABLE 1

Structure of the megaspore wall

	MARSILEA	REGNELLIDIUM	PILULARIA
Shape of spore	elongated	nearly spherical	nearly spherical
Dimensions	.425×.750 mm (M. vestita—Campbell)	.6 mm	.4 mm (P. globulifera, calc. from Meunier)
Endospore (shape)	elongated	nearly spherical	pear shaped
Inner epispore	thin	thin	much thicker than endo., esp. toward papilla
Prismatic layer	uniform thickness except papilla; there thin	uniform thickness except papilla; about 2× Marsilea	much thickest toward papilla, there thinner
Outer epispore	may be thickest toward papilla; not markedly papillate	uniform thickness, strongly papillate	much the thickest layer, not papillate
Mucilaginous layer	present	present	present
Papilla (apical)	3 radiating ridges (Campbell)	irregularly folded or lobed	longitudinally ridged (Meunier)

different from those in a plant with the habit of *Selaginella*. The slight degree of relationship between the two families of water-ferns is indicated in the pattern of the spore wall quite as plainly as in other parts of the plants; in both *Azolla* and *Salvinia* the megaspore wall is provided with cup-shaped depressions, while in the three genera of Marsileaceae the "prismatic" layer is the distinctive feature. Although these three genera show the same wall layers (endospore, inner epispore, prismatic layer, outer epispore, also mucilaginous layer if this counts as part of the wall), the details are different. Table 1 offers a comparative view, showing that the megaspores of the three genera differ especially in (1) shape and size,

(2) thickness of the inner layer of epispore, (3) localization of a thick region of the prismatic layer and of outer epispore, (4) relative development of the papillate feature of the third layer of epispore, and (5) details of the apical papilla. In general it may be said that it is as easy to distinguish *Marsilea*, *Regnellidium* and *Pilularia* by sections through their megaspores as by their external characters such as number of leaflets. The spore wall of *Marsilea* appears to be less specialized than in the other genera.

As to the forces at play in laying down the prismatic layer, there are as yet very few data. The work of Wodehouse (1934) has made it exceedingly probable that the exine of pollen grains possessing a pitted surface owes this pattern to the deposit of oil droplets on the surface of the growing wall, restricting the activity of the plasmodium to the spaces between these droplets. While this theory may have application in such cases as *Salvinia*, it offers no explanation of the production of radiating canals. Our curiosity regarding the radiating structure has been heightened when we have recalled the frequency of a prismatic layer in widely separated members of the living world, for instance, the prismatic layer of the sporocarp wall in all three genera of Marsileaceae, the similar layer in seed coats of certain Leguminosae (Russow, 1872), the inner layer of the shell in lamellibranchs, the dentine and enamel of the mammalian tooth. Is there possibly an underlying principle in these diverse instances? Strasburger (1882) studied thin sections of the developing wall in *Marsilea* and came to the conclusion that microsomes derived from the plasmodium become applied to the young spore wall in a radial arrangement corresponding to the radial pattern of the interprismatic substance. Recent work on cellulose molecules renders it probable that Strasburger's "microsomes" may soon receive a re-interpretation. As to the prisms, Campbell (1905) speaks of "close-set prismatic rods" in *Marsilea*. Several years earlier, Strasburger (1882) stated that the developing prismatic areas are filled with a weakly refractive liquid, which later gives place to air. He considers that this condition enables the spores to float on water, an idea that has no doubt occurred to others. Sachs (1875) evidently thought the layer to be really prismatic in *Pilularia*, but Meunier (1888), working with fresh material, insists that the radiating appearance is due to cavities filled with gas. Besides functioning as a floating device in the mature condition, it is possible that the immature wall serves a conducting function. The extent to which materials must pass through the spore-wall after the various layers are organized may be realized by an inspection of figure 29. This nearly mature spore contains a rather thin layer of starch grains, and the wall has not attained quite its full thickness, although the prismatic layer

is well developed. It is of course possible that the wall at this stage does not contain enough suberin to prevent passage of carbohydrates, etc., which evidently enter the spore and build up the starch grains and oil globules in quantity to eventually fill the cavity. The apical papilla is probably the most pervious region of the wall, as is indicated by the rapid development of the gametophyte. Perhaps we see here a meaning of the radiating canals or spaces—the so-called prisms. As the spore ripens the chemical nature of the wall may change with deposit of suberin and the wall may assume the character of a floating device.

Concerning the relationships among the three genera of Marsileaceae, there is every reason to consider that *Pilularia* represents reduction stages culminating in *P. minuta*. This is indicated not only by the lack of leaflets but by the small number of soral canals and of sporangia. In *Marsilea* the four leaflets may be regarded as primitive, also the large number of sporocarps (2–20), and perhaps the large number of soral canals (8–10 on each side). The megaspore wall is moreover simplest in this genus, being specialized in one respect in *Regnellidium* and in another in *Pilularia*. On the other hand the venation of the leaves is strictly dichotomous in *Regnellidium*, while frequent anastomoses occur in *Marsilea*. Surely the mucilaginous ring which bears the liberated sori in the latter genus should be regarded as a feature of specialization, absent in the other genera. Moreover the dichotomous plan of venation in the sporocarp is more clearly expressed in *Regnellidium*, probably on account of the location of attachment of stalk to capsule (see Johnson and Chrysler, 1938). This clearly expressed dichotomy extends to the origin of the vascular bundles supplying the sori. Thus it is difficult to reach a conclusion as to which genus comes nearest to the terrestrial ancestor. But the view may be entertained that *Regnellidium* represents an ancient and unprogressive member of the group, showing certain features of reduction, while *Marsilea* is the progressive member which has worked out such devices as the mucilaginous ring and a branching (chorisis?) of the sporocarp. At any rate *Marsilea* has become cosmopolitan and includes over fifty species, while *Regnellidium* is monotypic, a tropical endemic, perhaps relic.

A survey of the new evidence appears to give little reason for departing from the current opinion that the nearest relatives of Marsileaceae are Schizeaceae, in spite of some features suggestive of Cyatheaceae. Probably the most serious drawback to the schizeaceous alliance is the "monosporangiate sorus" of the Schizeaceae. This however may represent a special feature of the modern members of this family which was not present when the Marsileaceae branched off.

SUMMARY

1. The sporangia of *Regnellidium* exhibit a slight acropetal succession on the soral ridge, the base of which is considered to be the dorsal end where the vascular bundle enters.

2. The apical cell of the microsporangium is dolabriform, a feature which is regarded as a point of contact with Schizeaceae.

3. The micro- and mega-sporocytes are normally sixteen in each sporangium. A single megasporocyte ripens only one of its resulting spores, although several sporocytes of a sporangium may begin development, also two or more of the members of a tetrad may make some headway.

4. In the megasporangium the primary tapetum cuts off an external layer consisting of flat watery cells which are notably persistent. The inner cells divide in all three planes to form a 2–4 layered true tapetum, which fuses into a periplasmodium at about the time of separation of the spores. The plasmodium is richly provided with nuclei which appear to be active in building up the epispore.

5. The megaspore wall comprises: (1) endospore, (2) inner layer of epispore, (3) thick "prismatic" layer of epispore, (4) outer layer of epispore, the papillate form of the last being characteristic of the genus, as is also the shape of the apical papilla.

6. An epispore normally forms around each microspore, but occasionally surrounds a whole tetrad or even two tetrads. The microspore possesses a prismatic layer, and an apical papilla with remnants of the triradiate scar.

7. In general the features exhibited by *Regnellidium* are considered to strengthen the case for an alliance with Schizeaceae.

BUREAU OF BIOLOGICAL RESEARCH
RUTGERS UNIVERSITY
NEW BRUNSWICK, N. J., AND
THE JOHNS HOPKINS UNIVERSITY
BALTIMORE, MARYLAND

Literature cited

Bartoo, D. R. 1929. Development of sporangium in *Schizaea rupestris*. Botan. Gazette **88**: 322–331.

Binford, R. 1907. The development of the sporangium of *Lygodium*. Botan. Gazette **44**: 214–224.

Bower, F. O. 1926. The ferns. 3 vols. Cambridge.

Campbell, D. H. 1904. Affinities of the Ophioglossaceae and Marsileaceae. Amer. Nat. **38**: 761–775.

————. 1905. Mosses and ferns. 2d edition. New York.

Eames, A. J. 1936. Morphology of vascular plants, lower groups. New York.

Foster, A. S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. Stain Tech. **9.**

Hanstein, J. 1865. Die Befruchtung und Entwickelung der Gattung *Marsilia*. Jahrb. wiss. Bot. **4:** 197–260.

Johnson, D. S. 1898. On the development of the leaf and sporocarp in *Marsilia quadrifolia* L. Annals Bot. **12:** 119–145. *pl. 10–12.*

————, **and Chrysler, M. A.** 1938. Structure and development of *Regnellidium diphyllum*. Amer. Jour. Bot. **25:** 141–156.

Kundt, A. 1911. Die Entwicklung der Micro- und Macrosporangien von *Salvinia natans*. Beih. bot. Centralb. **27:** 26–51. *pl. 6, 7.*

Lindman, C. A. M. 1904. *Regnellidium* novum genus Marsiliacearum. Ark. för Bot. **3**(6): 1–14.

Marschall, Cornelia C. 1925. Differentiation of sporangia in *Marsilia quadrifolia*. Botan. Gazette **79:** 85–94.

Meunier, A. 1888. La Pilulaire. Étude anatomico-genetique du sporocarpe chez la *Pilularia globulifera*. La Cellule **4:** 319–400.

Russow, E. 1872. Vergleichende Untersuchungen der Leitbündel-Kryptogamen. Mem. Acad. Imp. Sci. St. Petersbourg **19:** 1–207. *pl. 1–11.*

Sachs, J. 1875. Text-book of botany, trans. Bennett and Dyer, Oxford.

Shattuck, C. H. 1910. The origin of heterospory in *Marsilia*. Botan. Gazette **49:** 19–40. *pl. 3–6.*

Smith, G. M. 1938. Cryptogamic Botany, vol. 2. New York.

Stevens, W. C. 1911. On the development of the sporangia and spores of *Anemia phyllitidis*. Annals Bot. **25:** 1059–1068. *pl. 84, 85.*

Strasburger, E. 1882. Ueber der Bau und das Wachstum der Zellhaute. Jena.

Tupper-Carey, R. M., and Priestley, J. H. 1923. The composition of the cell-wall at the apical meristem of stem and root. Proc. Royal Soc. **95B**: 109–131.

Wodehouse, R. P. 1929. The origin of symmetry patterns of pollen grains. Bull. Torrey Club **56:** 339–350.

————. 1934. An oil-drop theory of pollen-grain pattern formation. Amer. Jour. Bot. **21:** 18–22.

Studies on Rhizophidium. III. Germination of the Resting Spores

J. S. KARLING

(WITH PLATE 6)

Rhizophidium is the largest of the rhizidiaceous chytrid genera and at present is reported to include approximately fifty-five species, a large number of which are doubtful or imperfectly known. A survey of the literature shows that resting spores have been found in only twenty-one species and that germination has been seen in but three of these. In the course of a study on members of this genus a saprophytic species was found on dead cells of *Hydrodictyon reticulatum* whose resting spores germinated readily under laboratory conditions. The identity of this species is uncertain, but the shape and size of its zoosporangia are similar to those of *R. sphaerocarpum* and *R. globosum*. Since there are many similar species which will infect dead algal cells and other plant tissues, I hesitate to assign a specific name to the species at hand before a more intensive study of its development, structure, cultural characteristics, host range, etc., has been made.[1]

The mature resting spores are predominantly spherical, 8–15μ in diameter, but slightly oval and ellipsoidal spores, 5×7μ–10×14μ, also occur. They usually contain a large refractive globule in the center, which may often be more than half as large as the spore itself. The wall is amber to dark brown, smooth or rough, and varies from 2–3.5μ in thickness. The thickening and roughening of the wall can be followed readily in living material, and frequently when two or more spores occur close together, their adjacent walls fuse as the thickening proceeds, as is shown in figures 2 and 7. Figure 2 shows three spores in optical section with their adjacent walls united in the center.

Hyaline empty vesicles have often been found adhering to the sides of the spores, as is shown in figures 5 and 6. Such structures have been interpreted by Scherffel (1925), Couch (1932), and Sparrow (1933, 1935, 1936) as remains of male thalli which have fused with female thalli to form the resting spores. So far, I have not observed such fusion in this species, and the significance of the empty hyaline vesicles remains to be seen.

The resting spores germinated readily under the laboratory conditions of this study. As many as fifteen spores have been found germinating at the same time on a single host cell. The first stages were found five days after the spores were formed, and within fifteen days about 80 per cent had germinated. Subsequent observations have shown that germination is not unusual in the laboratory during the winter and spring months and

[1] The identity of this species and the evidence of sexuality are being investigated at present and will be reported in a subsequent paper.

that no long period of dormancy is necessary. Whether such abundant germination is seasonal or dependent on certain edaphic conditions has not been determined. The *Hydrodictyon* cells on which the resting spores developed had previously been dried, bleached in the sun, stored for a month, and then placed in shallow dishes filled with water from the greenhouse tanks. Heavy infection occurred within four days. The dishes were kept on a table before an east window and thus received several hours of direct sunlight. During the nights the temperature frequently dropped below 30°C., so that the chytrid resting spores were thus subjected to a wide range of temperature during the course of twenty-four hours.

The first visible change preparatory to germination is the development of a small germ pore in the thick brown wall. This pore varies from 1–2.5μ in diameter according to present observations and may be readily overlooked unless seen in profile view (fig. 3). While the development is going on, the refractive globule in the center of the spore begins to change somewhat in shape, particularly on the periphery adjacent to the pore, and as the protoplasm slowly emerges through the pore, this change becomes more apparent. Figure 3 shows an early germination stage with a small, spherical mass of protoplasm growing out of the spore, which may readily be recognized as an incipient zoosporangium. The large refringent globule in the spore appears to have become eroded on its periphery adjacent to the pore, as if it were undergoing fragmentation in that region. Numerous small fragments of refringent material are present underneath the pore as well as in the incipient sporangium, and these seem to have arisen from the larger globule in the spore. The wall of the young developing sporangium at this stage is usually very thin and is scarcely perceptible as such, while the protoplasm may often be quite vacuolate. Later developmental stages are shown in figures 4 and 7B. The incipient sporangia are considerably larger, contain several conspicuous, irregular and spherical refringent bodies, and are enveloped by a delicate but visible hyaline wall.

Explanation of Plate 6

Fig. 1. Small smooth resting spore of *Rhizophidium* sp.

Fig. 2. Three large rough-walled spores in optical section.

Fig. 3. An early stage of germination in which the young sporangium is forming on the outside of the spore.

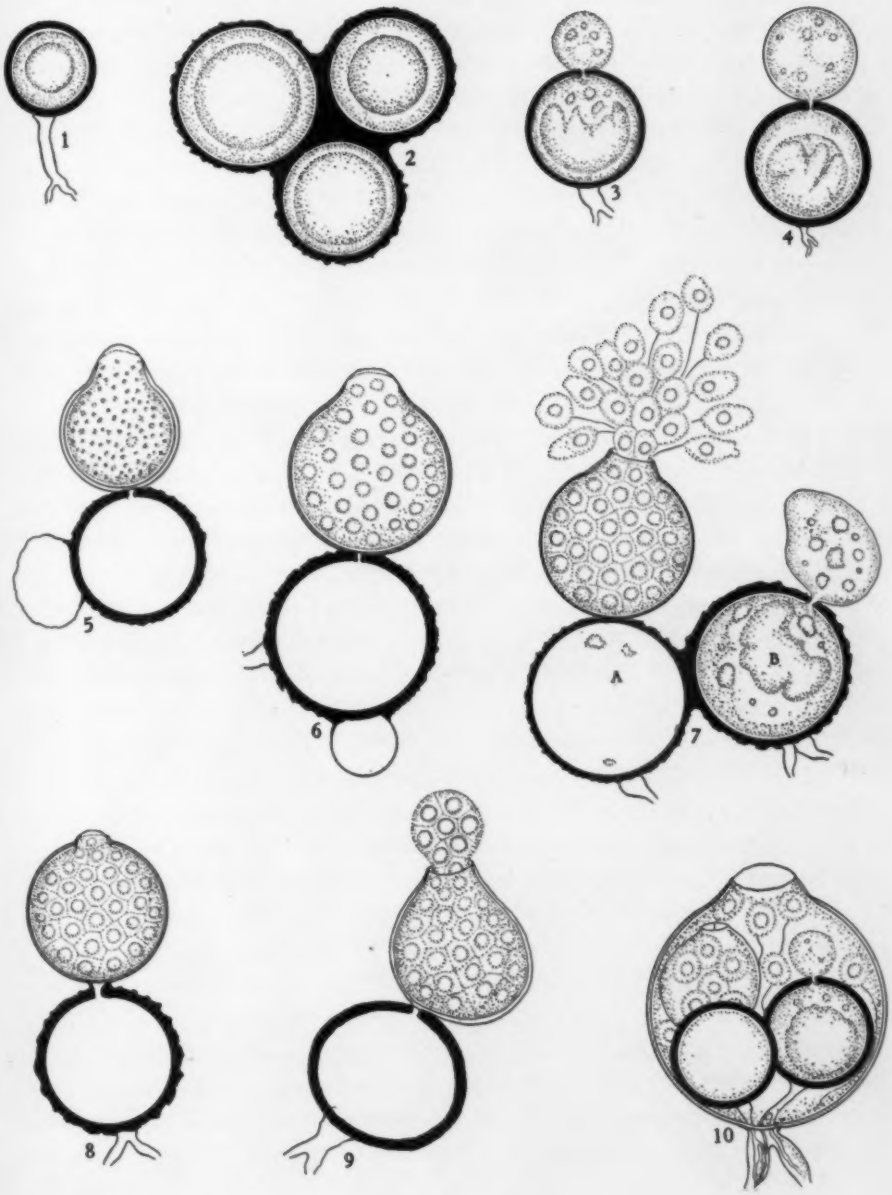
Fig. 4. A later stage.

Fig. 5. Completion of germination; the sporangium has attained its mature size.

Fig. 6 and 8. Stages in maturation and zoosporogenesis.

Fig. 7 and 9. Emergence and dispersal of the zoospores.

Fig. 10. Germination of two resting spores in an old sporangium.



KARLING: RHIZOPHIDIUM

The large globules in the spores have been reduced to about half their original size and become irregular in contour. The remainder of the protoplasm in the spores is highly vacuolate and consists largely of a primordial utricle. Occasionally at this stage the remnant of the large refringent globule may lie shrunken at the side opposite the germ pore.

The incipient zoosporangium continues to grow in size with the slow and gradual movement of the protoplasm out of the resting spore. This movement, however, is not sufficiently rapid to be observed with the oil immersion lens, and the complete development of the zoosporangium may require 8 to 16 hours. In the process of development the large refringent globule usually breaks up entirely, and its material passes out into the sporangium with the result that the resting spore may be completely emptied. Occasionally a few refringent segments may be left behind, as is shown in figure 7A. As development of the sporangium proceeds, the refringent material becomes more and more dispersed, so that by the time the zoosporangium has attained mature size, its protoplasm is somewhat evenly granular and grayish in color (fig. 5). The sporangium shown in this figure, though immature, is fully grown, possesses a well developed apical papilla, and has been delimited from the empty spore by a cross wall. Following this stage, the minute, highly dispersed refractive granules begin to coalesce, until finally a fairly definite number of conspicuous spherical globules are formed, as shown in figure 6. Within a short time the outlines of the zoospores become visible (fig. 8), and eventually the exit papilla deliquesces to emit the swarmspores (figs. 9, 7). The method of emergence and initial behavior of the zoospores are similar to those of the primary evanescent zoosporangia of other species of *Rhizophidium* (Karling, 1938), and it is unnecessary to recount the details here.

The mature sporangia vary from spherical in shape, 8–18μ in diameter, to ellipsoidal, ovoidal or pyriform, 5×7–10×18μ, and usually possess a single exit papilla. Figure 10 shows an old primary sporangium with two germinating resting spores within. These doubtless developed from zoospores which failed to escape and later germinated into thalli. The resting spore on the right has just begun to germinate, while in the one on the left germination and dehiscence of the sporangium are complete, and have given rise to the zoospores which are swimming about in the large old sporangium. Such structures as are shown in Figure 10 have been observed in three instances.

It is apparent from this description that resting spore germination in *Rhizophidium* sp. is fundamentally similar to that reported for *Polyphagus euglenae* (Nowakowski, 1877b; Wager, 1913), *Rhizidium mycophilum* (Nowakowski, 1877a), *Entophlyctis vaucheriae* (Fisch, 1884), *Chytridium*

Olla (De Bary, 1884), *C. Schenkii* (Sparrow, 1932), *C. lagenaria* (Karling, 1936), *Megachytrium Westonii* (Sparrow, 1933), *Diplophlyctis intestina* (Karling, 1936), and *Rhizidiopsis emmanuelensis* (Sparrow, 1936). The resting spore functions as a prosporangium, giving rise to a relatively thin-walled zoosporangium on its surface.

In *Rhizophidium ovatum*, however, Couch (1935) figures the resting spore or zygote as becoming transformed directly into a zoosporangium and thus giving rise to zoospores as in *Zygorhizidium Willei* (Lowenthal, 1905). Couch is not certain that his species belongs in *Rhizophidium*, and, as he suggests, it may possibly relate to the genus *Phlyctidium*. The same direct method of germination and zoospore formation has been reported by Dangeard (1900) for *R. transversum*, but this species may likewise belong in *Phlyctidium*, since he figures its absorbing system as consisting only of an elongated unbranched filament. It is to be noted in this connection that with the possible exceptions of Couch's and Dangeard's species, germination of the resting spores has never been reported in *Phlyctidium*. In another so-called *Rhizophidium* species, *R. messanensis*, Morini (1896) also figures the resting spores as forming zoospores directly without the development of a zoosporangium on its surface. This species, however, develops an extensive and branched rhizoidal system, so that it cannot be included in *Phlyctidium* as this genus is now recognized. In view of the fact that the main axis of its rhizoidal system is occasionally inflated like an apophysis, it may perhaps relate to *Phlyctochytrium*. If these three species do belong in *Rhizophidium*, it is apparent that two types of resting spores germination occur in this genus.

Literature cited

Couch, J. N. 1932. *Rhizophidium*, *Phlyctochytrium*, and *Phlyctidium* in the United States. Jour. Elisha Mitchell Sci. Soc. **46**: 231–239.

————. 1935. New or little known Chytridiales. Mycologia **27**: 160–175.

Dangeard, P. A. 1900. Le "*Chytridium transversum*" A. Braun. Le Bot. **7**: 282–284.

De Bary, A. 1884. Vergleichende Morphologie und Biologie der Pilze. Leipzig.

Fisch, C. 1884. Beträge zur Kenntniss der Chytridiaceen. Sitzb. Phys. Med. Soc. Erlangen **16**: 29–66.

Karling, J. S. 1936a. Germination of the resting spores of *Diplophlyctis intestina*. Bull. Torrey Bot. Club **63**: 467–471.

————. 1936b. The endo-exogenous method of growth and development of *Chytridium lagenaria*. Amer. Jour. Bot. **23**: 619–627.

————. 1938a. Studies on *Rhizophidium*. I. A large species of *Rhizophidium* from cooked beef. Bull. Torrey Bot. Club **65**: 439–452.

————. 1938b. Studies on *Rhizophidium*. II. *Rhizophidium laterale*. Bull. Torrey Bot. Club **65**: 615–624.

Lowenthal, W. 1905. Weitere Untersuchungen on Chytridiaceen. Arch. Protistk. **5**: 221–239.

Morini, F. 1896. Note micologiche. Malpighia **10**: 72–99.

Nowakowski, L. 1877a. Beitrag zur Kenntniss der Chytridiaceen. Beitr. Biol. Pflanz. **2**: 73–96.

————. 1877b. Beitrag zur Kenntniss der Chytridiaceen. II. Ibid. **2**: 201–219.

Scherffel, A. 1925. Zur Sexualität der Chytrideen. Arch. Protistk. **53**: 1–58.

Sparrow, F. K. 1932. Observations on the aquatic fungi of Cold Spring Harbor. Mycologia **24**: 268–303.

————. 1933a. Inoperculate chytridiaceous organisms collected in the vicinity of Ithaca, N. Y., with notes on other aquatic fungi. Mycologia **25**: 513–535.

————. 1933b. Observations on operculate chytridiaceous fungi collected in the vicinity of Ithaca, N. Y. Amer. Jour. Bot. **20**: 63–77.

————. 1935. Recent contributions to our knowledge of the aquatic phycomycetes. Biol. Rev. **10**: 152–186.

————. 1936. A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. Jour. Linn. Soc. Bot. **50**: 417–478.

Wager, H. 1913. The life history and cytology of *Polyphagus euglenae*. Ann. Bot. **27**: 173–202.

Flower Buds and Phylogeny of Dicotyledons

ALFRED GUNDERSEN

(WITH SEVEN FIGURES)

Differences of opinion regarding the classification of the dicotyledons have been many. Nevertheless, certain tendencies or directions of floral evolution have become almost universally recognized, such as those relating to sympetaly, to zygomorphy, to epigyny, to the fusion of carpels, and others. In many cases accepted views are definitely supported by the structure of flower buds. The present study relates largely to placentation.

PETALS: FROM SEPARATE TO UNITED

Flower buds and flowers in different families are illustrated by Maud H. Purdy in Figure 1. Comparing the bud of *Azalea* (*Rhododendron indicum*), 1 mm. long, with the flower, 30 mm. long, we note that in the bud the separate parts of the corolla are about four-fifths of its total length; in the flower they are only one-third of the length. In *Plumbago capensis* the bud, 1 mm. long, has separate parts about three-fourths the length of the corolla; in the flower, 20 mm. long, they are only one-eighth of its length. In *Forsythia viridissima* the bud, 3 mm. long, has separate parts about three-fourths of its length; the flower, 10 mm. long, has the separate and fused parts about equal. In the bud of *Lonicera fragrantissima*, 3 mm. long, the separate parts are about four-fifths of its length; in the 10 mm. flower the separate and united parts are about equal. These examples might be extended indefinitely. In each case the petals of the sympetalous flower are more nearly separate in the bud than they are in the adult flower. In other words, the growth occurs mainly in the lower, fused part, with the result that in the adult flower we have corolla lobes rather than petals. It is agreed that the upper, divided part of the corolla represents the early stage; the lower, fused part the advanced stage of floral evolution.

PETALS: FROM ACTINOMORPHY TO ZYGOMORPHY

Figure 1 at the same time illustrates the development of zygomorphy. The *Azalea* bud of 1 mm. is practically actinomorphic, in the flower zygomorphy is evident. Likewise in *Lonicera* zygomorphy is much more in evidence in the flower than in the bud. Among the polypetalous families comparatively few are zygomorphic; such are most Leguminosae, Resedaceae, Violaceae, Polygalaceae, Balsaminaceae and others. But in the Sympetalae numerous families are typically zygomorphic. In the flower of Leguminosae one stamen is usually separate from the others, in the young bud they are practically similar to one another. For example, in

the bud of *Clitoria Ternatea*, when less than 1 mm., the ten stamens are nearly alike, the large anthers having hardly any filaments. The development is always toward zygomorphy, never the opposite.

SEPALS: FROM SEPARATE TO UNITED

While much has been written about sympetaly, synsepaly has received little attention. The development of sepals is like that of petals, that is, in synsepalous flowers the separate sepals are more prominent in the bud than in adult flowers. We conclude that polysepaly is the primitive, and synsepaly the derived form. Separate petals occur in a great majority of the dicotyledons, but separate sepals are found in comparatively few families. These are nearly all in three groups: Ranales, Papaverales and Parietales, groups which are also for other reasons suspected of being primitive.

OVARY: FROM SUPERIOR TO INFERIOR

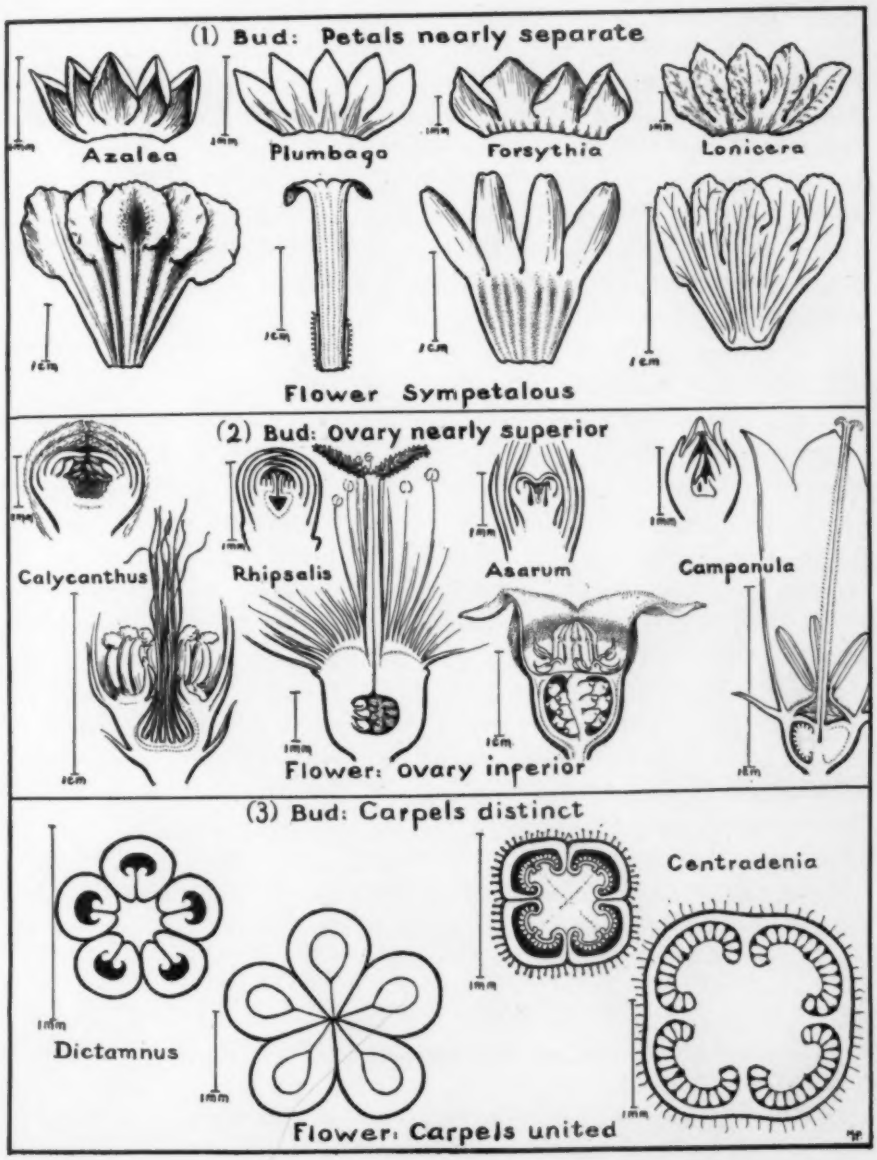
In Figure 2 *Calycanthus fertilis* represents a perigynous flower. In the bud the depth of the ovaries is about one-half the cross-section above them, in the flower the depth is about four times that section. In the bud of *Rhipsalis rhombea* the ovary is approximately on the level of the perianth, but the flower is definitely epigynous. In the bud of *Asarum canadense* the young carpels together with the stamens are raised above the base of the perianth; in the flower there is a definite inferior ovary. In the *Campanula rotundifolia* bud the beginnings of the carpels show similar difference with the adult flower. It appears to be a general fact that in buds of epigynous flowers the ovary is more nearly superior than in the adult form. Epigny is recognized as being more advanced than hypogyny. The greater protection of the ovules must be considered an advantage to their development.

CARPELS: FROM SEPARATE TO UNITED

In Figure 3 the bud of *Dictamnus albus* shows the carpels nearly separate, with a considerable central space. When the diameter has enlarged about three times the carpels are nearly fused. In the bud of *Centradenia floribunda* the carpel lines are distinct, in the flower they are obliterated. Separate and open carpels in the young bud is the usual condition. The style is always very slightly developed in the bud. However, a few adult flowers do have somewhat open ovaries, notably *Reseda*, *Platanus* and Cactaceae.

Separate carpels are usual in the *Magnolia* and *Rosa* groups of families, outside of these they are unusual. But in numerous families we have separate stigmas. As these are the first to appear in the bud, they may reason-

ably be considered as the remains of former separate carpels, analogous to the corolla lobes of Sympetalae. Hallier, Arber and Parkin, Bessey, Wie-



Figs. 1–3. Flower buds and flowers compared.

land (13), Eames (4) and others have presented strong and varied evidence showing that plants with separate carpels should be considered the basal group for at least a majority of dicotyledons.

PLACENTATION: HISTORICAL

From the above illustrations of the principle that ontogeny recapitulates phylogeny, we pass to a subject not so generally agreed upon, namely placentation. The involved changing views as to placentation deal largely with central placentation, the history of which has been outlined by Douglas (3). Occupied with the axial versus appendicular discussion, Payer (8), in 1857 considered *Polygonum*, *Chenopodium* and *Primula* as exhibiting the simplest form. From his drawings, however, numerous examples are seen of flowers with axile placentation which in the bud have open centers similar to those of flowers with parietal placentation. In 1874 Eichler wrote in his *Blütendiagramme* "The whole question of placenta formation deserves a new investigation, both from a developmental and from a systematic-comparative point of view."

Engler wrote in his *Syllabus:* When in a related group there is only parietal placentation, it is not necessary to assume that this is a progression from a many-celled ovary; for as soon as syncarpy arose, either a many-celled or one-celled ovary might develop, according as the carpel margins were more or less bent inward." Diels (2) stated, in 1920, under *Organisationshöhe und Progression der Merkmale:* "Ovary cells as many as the carpels to less than these." These statements together with the placing of *Parietales* so high in the Engler system suggest that parietal placentation is considered to be a derived form. Placentation is not referred to in the list of evolutionary tendencies by Bessey (1914). But the parietal-axile sequence of placentation is accepted by Sprague (9) in his *Classification of Dicotyledons* (1925). Though Hutchinson does not include placentation in his principles of classification in his book *Families of Flowering Plants*, (7), the same year (1926), he stated at the Ithaca Congress: "After syncarpy was attained, the parietal type of placentation generally preceded the axile, basal, or apical types, the axile being the final and most efficient condition." But this principle is given little attention in his system.

PLACENTATION: FROM PARIETAL TO AXILE

The genus *Hypericum* has two kinds of placentation, parietal and axile. *Hypericum gentianoides, H. ellipticum* and others have a one-celled ovary with three parietal placentae. In these species the young ovaries have open centers the same as the adult forms. The development of axile placentation of *Hypericum densiflorum* is shown in Figure 4. To the left the ovary is half a millimeter in diameter and shows essentially parietal placentation. In the longitudinal section of the bud we note that at this stage the placentae are fused only at the base. To the right, the ovary, at

a later stage is shown with a diameter about three times larger. Here we have axile placentation; in the longitudinal section we note that only the top part has an opening in the center. *Hypericum perforatum* and other species with axile placentation show similar development. If this is a case where ontogeny recapitulates phylogeny, we must consider the species having parietal placentation to be the primitive ones.

The development in *Theobroma Cacao* (Sterculiaceae) is shown in Figure 5. In the longitudinal section we note the open part above, the fused part below. The open part between the placentae, conspicuous in the bud, gradually disappears in the flower, and we have axile placentation. Figures 6–8 show similar development in Zygophyllaceae (*Peganum harmala*), Hydrangeaceae (*Philadelphus coronarius*), Scrophulariaceae (*Verbascum Thapsus*) and Iridaceae (*Iris pumila*).

In general, the cross-section of young ovaries of flowers with parietal placentation is about the same as in the adult flower. But not so with those having axile placentation. Among the numerous genera which have open centers in the bud may be mentioned *Hibiscus*, *Tilia*, *Gordonia*, *Ruta*, *Ilex*, *Linum* and *Tropaeolum*. In all cases the change or suggestion of change is from parietal to axile placentation, never the reverse. In a number of cases, for example *Shortia*, *Feijoa* and *Myrtus*, the upper part of the ovary has parietal placentation, the lower part axile. The reverse does not occur. Here, as with the petals, we must consider the upper part to represent the primitive condition.

Among Sympetalae parietal placentation is rare, in itself a suggestion that is is a primitive character. Gentianaceae, except *Exacum*, have parietal placentation. But the bud of *Exacum* has at first open center like that of *Gentiana*, axile placentation gradually developing. In the *Natürliche Pflanzenfamilien*, the Gentianaceae begin with *Exacum* because of its axile placentation, but a terminal position would be preferable.

In many families such as Papaveraceae, Cactaceae, Gentianaceae and others, we find numerous small seeds associated with parietal placentation. Many stamens and many small seeds are in general primitive characters. Advanced flowers such as those of Labiatae and Compositae, have few stamens and few seeds or a single seed per flower.

PLACENTATION AND CLASSIFICATION

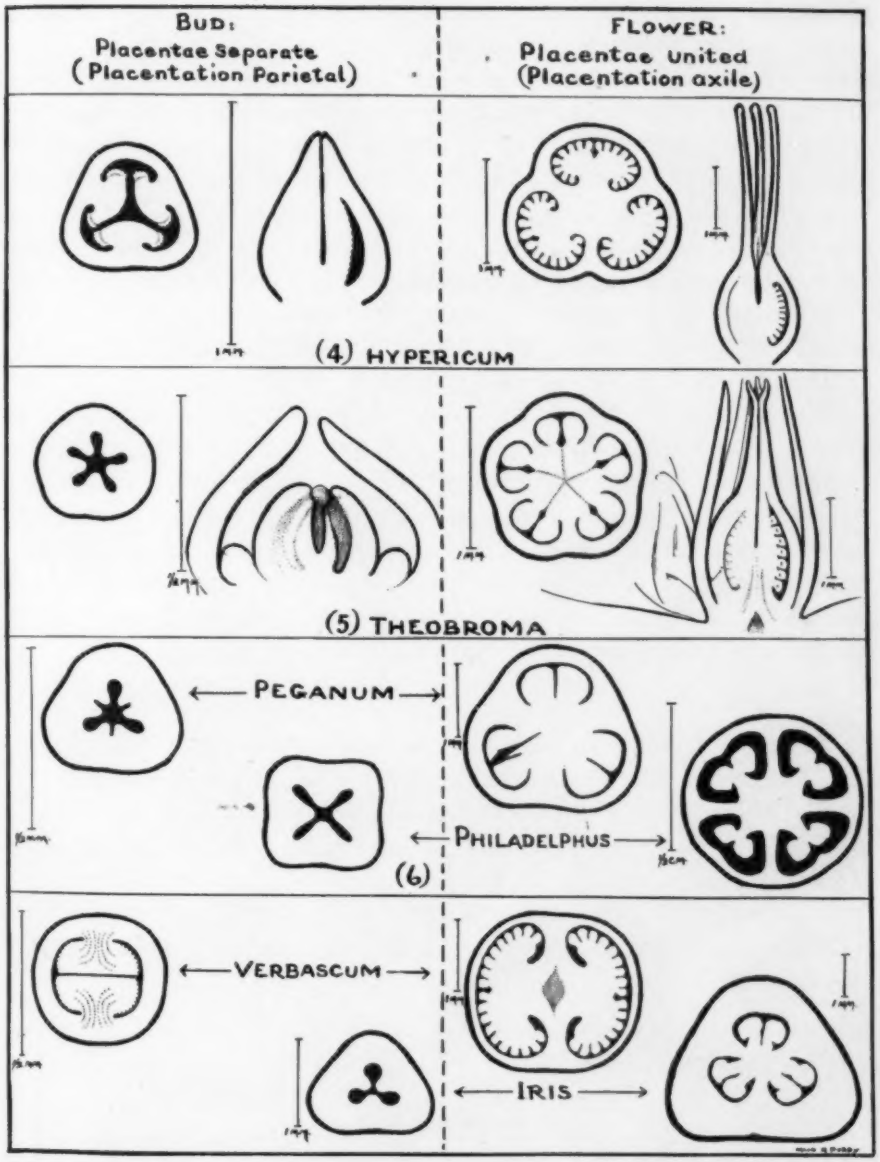
Families of Parietales with spirally arranged flower parts, numerous stamens and other primitive characters connect on the one hand closely with the Ranales of the Engler system, on the other hand with the Papaver group of families. In particular the families Cistaceae and Papaveraceae have many characters in common. In the systems of Jussieu,

DeCandolle, Bentham and Hooker, and Eichler they are near together. But in the Engler system Parietales come between Malvales and Opuntiales. The separation of Parietales from Papaverales is a peculiarity of the Engler system, though Engler also accepted their affinity as seen in his suggestive diagram (5) of 1897. At the same time he wrote that his order Parietales is a complex of groups of different origins which have arrived at a similar morphological state (meaning parietal placentation?). In the later systems of Warming, Wettstein, and Bessey *Cistus* and *Papaver* have again been brought near together, rightly we think. Even Rendle, whose *Classification of Flowering Plants* (9) follows approximately the Engler system, departs from it in this respect and adopts the arrangement *Rhoeadales*, *Sarraceniales*, *Parietales*. Mez wrote in 1926, "Large branches of the dicotyledon system are derived from the region of the Parietales, these stand exceedingly close together." Mez places the *Papaver* group near Parietales. Tippo (12) has made suggestions for the relationships of supposed primitive dicotyledons; axile placentation is almost entirely absent among these families. Wilson (14) points out primitive characters of stamens in Parietales and Malvales. F. H. Taylor (11) stated recently (1938), "Anatomically, Violaceae and Flacourtiaceae (Parietales) exhibit numerous primitive features, whose discovery is definitely interesting in dicotyledons placed high in the Archichlamydeae,"—"in the Engler system" should have been added.

Cactaceae usually have parietal placentation, though *Pereskia* has basal ovules like *Tamarix*. The resemblance of flowers of Cactaceae and Nymphaeaceae is well known. They also resemble Myrtaceae; the presence of Myrtaceae in the Cretaceous period, and also their Australian distribution make affinity with Cactaceae more reasonable if the Cactaceae themselves are primitive. The Cactaceae are specialized, so far as vegetative characters are concerned. Many characters connect Cactaceae with *Mesembryanthemum* and with Portulacaceae (Chorinsky, 1); these suggest changes from parietal to axile and to central placentation. Though Engler accepted the affinity of Cactaceae to *Mesembryanthemum*, this idea was not carried into his system.

Tamaricaceae and Frankeniaceae are families with basal or parietal placentation. *Frankenia*, in numerous characters so near *Dianthus*, has in different species parietal and basal placentation. Frankeniaceae and Caryophylaceae were placed together in the Bentham-Hooker and older systems. Together they make a reasonable connection to families with central placentation (6). The position of these families in the Engler system is especially unsatisfactory.

It does not seem desirable to use the terms pistil or placentation in



Figs. 4–7. Placentation in flower buds and in flowers.

speaking of plants like *Magnolia*, *Ranunculus*, *Rosa* or *Berberis*, with carpels separate or single. For these plants the term carpel is preferable, thus limiting the word pistil to flowers with fused carpels. Placentation we consider to relate to the structure of fused carpels only. Primitive

placentation means placentae fused by two's along the margins of adjacent carpels, that is, placentae in separate groups; but axile placentation means more extended placentae united in the center. Axile placentation is an improvement on parietal placentation in somewhat the same way that epigyny is an improvement on hypogyny, for the growing ovule needs nourishment and protection, and these requirements are better supplied in epigyny and in axile placentation than in hypogyny and in parietal placentation. We have thus for placentae essentially the same development as for petals, sepals, or carpels, namely, from separate to united parts. Carpels from separate to united, placentae from separate to united, and petals from separate to united appear to briefly summarize stages of various phylogenetic lines of floral evolution.

The terms ovary and placenta have been taken over from zoology to botany because of similarity of function, the ovary to contain, the placenta to nourish the growing organism, whether animal or plant. In zoology, the coming of placental mammals marks a definite step in evolution, namely increasing care of the next generation. In botany the term ovulary has been proposed. Whatever the name, to assign to placentation a more important place in the classification of the higher plants calls attention to a significant analogy between plant and animal evolution.

SUMMARY

For many characters, such as sympetaly, zygomorphy and epigyny, the ontogeny of flowers confirms accepted views of phylogeny.

But while flowers with parietal placentation are similar in the bud and in the adult form, those with axile placentation usually have a beginning of parietal placentation in the bud.

If groups with parietal placentation, such as Opuntiales, Parietales and Papaverales, are placed together early in the system the classification becomes more natural.

BROOKLYN BOTANIC GARDEN
FEBRUARY, 1939

Literature cited

1. **Chorinsky, F.** 1931. Untersuchung der Haarbilde bei Portulacaceen und Cactaceen. Ost. Bot. Zeit. **80**: 308–327.
2. **Diels, L.** 1920. Die Methoden der Phytogeographie und der Systematik der Pflanzen, p. 145. In Abderholden, Handbuch der biol. Arbeitsmethoden.
3. **Douglas, G. E.** 1936. Studies in vascular anatomy of the Primulaceae. Am. Journ. Bot. **23**: 199–212.
4. **Eames, A. J.** 1931. The vascular anatomy of the flower. Am. Journ. Bot. **18**: 147–188.

5. **Engler, A. and Prantl, K.** 1897. Die näturlichen Pflanzenfamilien; Nachträge II–IV: 376. Leipzig.
6. **Gundersen, Alfred.** 1927. The Frankeniaceae as a link in the classification of dicotyledons. Torreya **27**: 65–71.
7. **Hutchinson, J.** 1926. Families of flowering plants: Dicotyledons. London.
8. **Payer, J. B.** 1857. Traité d'Organogénie comparée de la fleur. Paris.
9. **Rendle, A. B.** 1925. The classification of flowering plants. II. Dicotyledons. Cambridge.
10. **Sprague, T. A.** 1925. The classification of dicotyledons. Journ. Bot. **63**: General principles p. 9; Evolutionary progressions p. 105.
11. **Taylor, F. H.** 1938. Comparative anatomy . . . Violaceae and Flacourtiaceae. Botanical Society of America, Richmond. (Abstract).
12. **Tippo, O.** 1938. Comparative anatomy of the Moraceae and their presumed allies. Bot. Gazette **100**: 1–99.
13. **Wieland, G. R.** 1934. Wood anatomy and angiosperm origin. Tropical woods **39**: 1–11.
14. **Wilson, C. L.** 1937. Phylogeny of the stamen. Am. Journ. Bot. **24**: 686–699.

Lagenospermum imparirameum sp. nov., a Seedbearing Fructification from the Mississippian of Pennsylvania and Virginia[1]

CHESTER A. ARNOLD

(WITH TEN FIGURES)

The fructifications described in this account are the first of their kind to be recognized in the Mississippian (Lower Carboniferous) of North America. Previous descriptions of the flora have dealt mainly with vegetative remains. Fructification material has been found recently at several places, but the largest quantity was collected from an outcrop of the Pocono in the railway cut west of the bridge (known as High Bridge) over Fishing Creek about one fourth of a mile west of Outwood, Schuylkill County, Pennsylvania. At this place the plantbearing beds are accessible along the south side of the track in a vertically tilted stratum of dark gray shale which is about one hundred feet thick and flanked on either side by massive sandstone. The best material was secured in 1936 when a large number of seeds were found in a thin zone near the eastern extremity of the exposure. During two later visits to the place only a few were found. A goodly quantity of specimens was also collected from the black shale of the Price formation on the dump of the Merrimac mine near Blacksburg, Virginia, and a few isolated seeds are present among a small collection of Pocono plants from Allegrippus west of the Horseshoe Curve in Blair County, Pennsylvania.

The Pocono and Price formations are of similar age, and constitute the basal members of the Mississippian in the Appalachian region. The distribution of *L. imparirameum* indicates that it may be one of the characteristic species of plant fossils in these formations.

The fructifications are small, terminal, seedbearing husks on bifurcated stalks of slightly unequal length (Figs. 1–8). Their affinities are apparently with the lyginopterid group of the Pteridospermeae and they appear to fall within the confines of *Lagenospermum*, a genus instituted by Nathorst for fructifications which resemble *Lagenostoma* but lack internal structure. They are also referable to Goeppert's form genus *Calathiops* (4), although this seems less desirable for reasons to be discussed. Goeppert's diagnosis of *Calathiops* is brief and the name was proposed

[1] Paper from the Museum of Paleontology and the Department of Botany of the University of Michigan. The material was described before the Paleobotanical Section of the Botanical Society of America at Indianapolis, Indiana, on December 28, 1937, under the title *The Morphology of Calathiops and Its Occurrence in North America.* (Abstract in Amer. Jour. Bot. vol. **24**, p. 743. 1937.)

merely for naked, subdichotomously branched axes bearing terminal tufts of basally joined lanceolate-linear bractlets which may sometimes enclose a seed. Goeppert, however, observed no seeds in his material, and the name has subsequently been applied to several indeterminate fructifications answering this brief description. Some of the fructifications which have been placed in *Calathiops* are probably pollenbearing organs. Therefore, since an assignment to *Calathiops* does not imply either a seed or a spore producing organ, a fructification in which the contents are known should preferably be assigned to some other genus. Goeppert's account of *Calathiops* was included in a large work dealing primarily with Permian plants, and consequently the name was long overlooked as a generic cate-

Fig. 1. Seed cupules borne upon pedicels of unequal length, ×about 2.

Fig. 2. Pair of cupules showing a seed only slightly displaced from its original position, ×about 1½.

Fig. 3. Cupule pair borne upon very short unequal pedicels, ×about 2.

Fig. 4. Specimen similar to that shown by Fig. 1, ×about 1½.

Fig. 5. Single well preserved cupule, ×about 1½.

gory for early carboniferous or Devonian fructifications. Otherwise many forms which have received such names as *Schuetzia*, *Alcicornopteris*, *Ptersispermostrobus* or *Xenotheca* might have been referred to it.

The stalks which bear the seed husks of *Lagenospermum imparirameum* branch dichotomously. The terminal cupules are produced either upon slender, leafless stalks resulting from a single bifurcation (Figs. 1, 2, 4, 5, 6, 7) or in pairs upon very short stalks resulting from a secondary forking (Fig. 3). A single primary stalk may therefore bear two, three or four cupules, depending upon the number of ultimate branches. The branches resulting from the first bifurcation are 1 mm. or less in diameter, and range up to 12 mm. in length. If secondary branching occurs, the branches

are always short and the two terminal cupules are borne in such close proximity that they often appear as a single fructification which is somewhat broader than the ordinary ones (Fig. 3). Even in such fructifications, however, the unequal dichotomy is visible because one cupule of the pair is usually slightly lower than the other, giving the false impression of a single body with an oblique base.

The individual cupules are about 3 mm. wide and 9–10 mm. long, and appear to consist of five slender bracts joined basally for about two thirds of their length. Within the cupule the seed is borne. The free ends of the bracts extend beyond the seed as sharp tapering points. It is evident, therefore, that the cupule of *L. imparirameum* is similar to that of the well known *Lagenostoma Lomaxi* (except for the lack of the capitate glands which characterize that species) and the plant which bore it is probably a member of the Lyginopterideae.

The exact manner in which the seeds were attached within the cupules is not apparent although each cupule appears to contain a single one (Fig. 8). The larger specimens which appear as if they might contain more than one seed should be interpreted (as previously explained) as a pair borne in close proximity on very short pedicels. These paired cupules are placed nearly parallel to each other, although they may be produced at slightly different levels.

Detached seeds have been observed among the cupules from High Bridge and the Merrimac Mine, as well as other places. One cupule from High Bridge shows a seed only slightly displaced from its original position (Fig. 2). The seeds are oval, and measure approximately 2 mm. in diameter and 5 mm. in length (Fig. 9). They are enclosed except at the tips by the joined bases of the surrounding bracts. Very little of the tissue of the seed is preserved except an amber colored surface membrane on which a rather characteristic reticulate pattern may be seen (Fig. 10). This pattern is so pronounced that it serves to identify the detached seeds at places where the cupules were not found.

That these oval bodies are seeds rather than spore cases is indicated by the fact that they produce shallow concavities filled with carbonaceous material in the dark shaly matrix. No spores have been found in the several specimens macerated. The form of the seeds is simple without the prominent testal angles or ridges which so frequently characterize Paleozoic seeds, although such features might have been obliterated by the extreme pressure to which these seeds had been subjected.

No foliage has been found attached to *L. imparirameum* although the leaf type recently described as *Cardiopteridium Holdeni* (7) is abundant wherever the seeds or cupules occur. A small slab from High Bridge bears

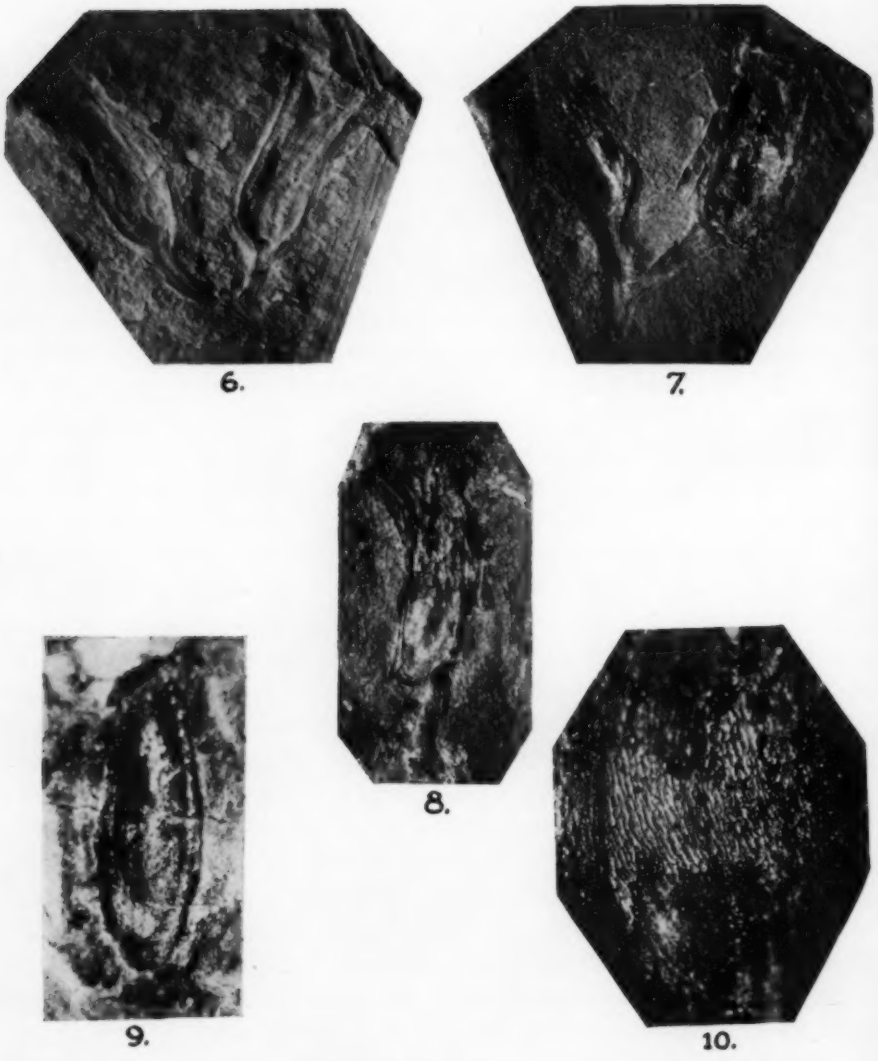


Fig. 6. Holotype specimen. From the Price formation, Merrimac Mine, Va. *No. 20798*, Univ. Mich. Coll., ×3.

Fig. 7. A specimen similar to that shown in Fig. 6, less well preserved but the position of the seed is shown in each capsule. Paratype. From the Pocono at High Bridge, Pa. Univ. Mich. Coll. *No. 20901*, ×3.

Fig. 8. Single cupule showing the outline of the compressed seed. Other data as for Fig. 7.

Fig. 9. Detached seed, ×about 7. Other data as for Fig. 7.

Fig. 10. Enlarged view of seed surface showing characteristic reticulations, ×20.

a pinnule which was probably attached to a seedbearing stalk, but a break in the matrix destroys the organic continuity if such existed. Several forms of *Triphyllopteris*, *Rhodea*, and *Adiantites* also occur, but not so intimately. The published figures of *C. Holdeni* are indistinct, but material collected at High Bridge and the Merrimac mine reveals its characters adequately.

The associated foliage (*C. Holdeni*) appears identical with that erroneously referred by Lesquereux in the *Coal Flora* (9, Pl. XLIX, Figs. 1–3) to *Archaeopteris Bochschiana* but transferred by Kidston (8, p. 414) to *Aneimites acadica*. The similarity extends to such features as the outlines of the pinnules, venation, mode of branching and especially to the long acutely tapering base of the terminal pinnule. The resemblance to Lesquereux's figures is so close that there can be no doubt about specific identity.

The previously described Paleozoic fructifications with which *L. imparirameum* may be compared are known under a variety of names. Were it not reasonably certain that the fructification bears seeds, *Calathiops* would be the appropriate name for it. However, a seed is definitely present, and as far as external appearances are of value in expressing affinities, the resemblance is certainly closer to *Lagenostoma* than to any other structurally preserved seed type.

Lagenospermum Sinclairi, described by Arber (1) from the Lower Coal Measures of Ayrshire, resembles *L. imparirameum* in the possession of a cupulate seed borne terminally on a naked forked pedicel. There is also some similarity in size and Arber states that the cupule of this form is 3 mm. broad by about 8 to 9.5 mm. in length. The seeds of the two forms are similar although no reference is made to surface configuration on *L. Sinclairi*. A slight difference may be noted in the length of the apical lobes of the cupules. Those of *L. Sinclairi* are said to be from 1.5 to 2.5 mm. whereas those of *L. imparirameum* may project for 3 or 4 mm. beyond the apex of the seed. The branching of *L. Sinclairi* is not so strictly dichotomous. Aside from these and other minor differences the two forms appear essentially alike.

Pterispermostrobus bifurcatus (Stopes, 10) from St. Johns, New Brunswick, resembles *L. imparirameum*, but in the absence of seeds this form must be retained within the *Calathiops* category. The campanulate seed cups of both forms consist of joined bracts which are free at the tips, but in *P. bifurcatus* the seedbearing pedicels are of equal length, and the bifurcated branches are spaced at intervals of about 1 centimeter along the main rachis. Also, as may be noted when measurements are compared, the cupules of *L. imparirameum* are slightly larger. Apparently the two

forms are the seedbearing organs of similar plants, although sufficient differences exist to denote specific separation.

Benson (3) and Gothan (6) have described a seedbearing structure under the name of *Calathiops Bernhardti*. This fructification differs from *L. imparirameum* in several important respects, and it probably belongs to a different group of pteridosperms. The cupules of *C. Bernhardti* are larger and the seeds are rounded bodies, and it differs further in that the cupules appear to be crowded into dense clusters on sympodially produced stalks. Gothan (5, Pl. I) also figures a specimen of *Calathiops plauensis* which closely resembles *L. imparirameum* after the seeds have become detached from the cupules. Although none of the cupules of *C. plauensis* reveal seeds, one cupule in particular shows an empty central area flanked on either side by fibrous bracts. The entire organ resembles a seed receptacle and the central space occupies the same position as does the seed of *L. imparirameum*. It therefore seems probable that *C. plauensis* is a seedbearing organ of the *Lagenospermum* type.

Paired objects resembling cupulate seed husks occur in the Upper Devonian of Pennsylvania (2). Although these organs bear a close resemblance to the Pocono fructifications, the presence of seeds in them has not been demonstrated. However, they more closely resemble seed husks than any other structures known from the Devonian.

Numerous references to *Calathiops*, *Telangium Calymmatotheca*, *Alcicornopteris* and *Schuetzia* may be found in the literature on early Carboniferous plants. For the most part these fructifications consist of terminal acicular bracts on dichotomously forked axes, and some are supposed to represent microsporangiate organs. It is interesting to note that among fructifications of this type the pollenbearing and the seedbearing structures are sometimes difficult to distinguish, and this similarity may have some bearing on the problem of the origin and evolution of the seed. It may be postulated that from the single, terminal sporangium of the psilophytalean type of the early Devonian, there developed during the later Devonian and the early Carboniferous, the *Calathiops* type of fructification. Some members of these bore microspores but others bore megaspores. By the retention and enlargement of the megaspore, the rather simple, terminal, cupulate seed of the *Legenospermum* type developed. *Telangium*, probably belonging to *Lyginopteris*, may be interpreted as the more completely differentiated microsporangiate organ which still resembles the primitive undifferentiated type of fructification by being borne terminally on leafless, bifurcated branches. These terminal, and bracteate or cupulate organs may therefore represent certain stages in the evolutionary development of the pollen producing and the seed producing organs. The terminal

position of these fructifications on bifurcated and leafless axes is comparable to that of the most primitive vascular plants known, the Psilophytales, and support is thereby lent to the recent hypothesis based upon paleobotanical evidence that the seed might have been a terminal organ at the time of its origin, and that it evolved independently of the leaf.

UNIVERSITY OF MICHIGAN

Literature cited

1. **Arber, E. A. N.** 1905. On some new species of Lagenostoma, a type of pteridospermous seed from the Coal Measures. Proc. Roy. Soc. London, B, **76**: 245–259.
2. **Arnold, C. A.** 1935. On seedlike structures associated with *Archaeopteris*, from the Upper Devonian of northern Pennsylvania. Contr. Mus. Paleont. Univ. Michigan, **4**: 283–286.
3. **Benson, M.** 1935. The fructification, *Calathiops Bernhardti* n. sp. Ann. Bot. **49**: 155–160.
4. **Goeppert, H. R.** 1864–65. Die fossile Flora der permischen Formation. Palaeont. **12.**
5. **Gothan, W.** 1927. Über einige Kulmpflanzen vom Kossberg bei Plauen i V. Abhandl. Säch. Geol. Landesanst., **5.**
6. ————. 1935. Die Steinkohlenflora der westlichen paralischen Steinkohlenreviere Deutschlands. Abh. Preuss. Geol. Landesanst. N. F. **167.**
7. **Jongmans, W. J., W. Gothan and W. C. Darrah.** 1937. Beiträge zur Kenntnis der Flora der Pocono-Schichten aus Pennsylvanien und Virginia. Compt. Rend. Deuxieme Congr. l'Avanc. étud. Stratr. Carb., Heerlen, 1935, **1**: 423–444. Maestricht.
8. **Kidston, R.** 1924. Fossil plants of the Carboniferous rocks of Great Britain, Mem. Geol. Surv. Great Britain, Pal., **2**(5): 377–522.
9. **Lesquereux, L.** 1879. Atlas to the coal flora of Pennsylvania and the Carboniferous formation throughout the United States. Harrisburg.
10. **Stopes, M. C.** 1914. The "Fern Ledges" Carboniferous Flora of St. John, New Brunswick. Canada Dept. Mines, Mem. 41.

Notes on the Botanical Components of Curare—II

B. A. Krukoff and A. C. Smith

The first paper in this series, discussing the botanical components of Curare as prepared by the Tecuna and Java Indians of Brazilian Amazonia, was published in 1937 (5). Dr. K. Folkers (1) has published preliminary chemical and pharmacological studies of the material obtained from the plants which were the basis of our botanical work. Now, through the courtesy of Mr. Richard C. Gill, we are able to examine specimens of the plant components of the Curare of the Canelos Indians of Ecuador. Specimens discussed in the present paper were collected by Mr. Gill on the Gill-Merrill Ecuadorian Expedition in August to October, 1938, having been obtained in the Pacayacu–Sarayacu region, drained by tributaries of Rio Pastaza in the Province of Napo-Pastaza. The collection is of unusual interest, since there appears to be no published record of the botanical identity of a single plant which the various Indian tribes of Ecuador use in preparing Curare. This is true in spite of the fact that many of these tribes, such as the Canelos, Jibaros, and others, are known to use blow-guns and Curare extensively and have been visited on many occasions by various explorers.

The crude material of plants used by the Canelos Indians in the preparation of the poison is now under chemical and pharmacological study in the Research Laboratory of Merck & Co., Inc., and at the Merck Institute of Therapeutic Research, Rahway, New Jersey. Botanical specimens mentioned in this paper are deposited in the herbarium of the New York Botanical Garden, unless otherwise noted. We take this opportunity to thank Prof. S. J. Record and Dr. R. A. Cockrell for their cooperation in checking our determinations of certain sterile plants on the basis of wood samples.

CURARE OF THE CANELOS

During his stay in the territory inhabited by the Canelos Indians, Mr. Gill had the opportunity to observe the preparation of Curare in several localities and by different poison-makers. He has kindly made available to us extensive notes regarding these preparations. Below we shall list the quantities, parts of the plants, and botanical names of the plant components of Curare as Mr. Gill saw it prepared in different localities. From these, as well as from several other "recipes" obtained by Mr. Gill but not given here because of space limitations, it is evident that the Canelos as a rule use the same main ingredients. The quantities and the secondary ingredients vary considerably from locality to locality and with different

poison-makers. These facts are also true, in a general way, of other South American tribes which prepare Curare.

We do not consider it worth while to discuss here the details of Curare preparation by the Canelos, since this subject has been covered by Karsten (3: 149–152) and others. However, we shall briefly call attention to the more important features of the preparation as observed by Mr. Gill. The ingredients, regardless of what portion of them is used, are thoroughly macerated and mixed together in large earthenware containers with an adequate amount of water. Thereafter the whole process consists of boiling until the Curare approaches its final stage and becomes thick and syrup-like. During this boiling, the mixture has been strained two or three times and the surface scum has occasionally been removed. The Curare is finally brought to the desired concentration in a small container over a very slow fire to guard against scorching.

The important feature of Curare preparation by the Canelos is that they use the macerated whole stems of their main menispermaceous ingredients rather than merely the bark. In addition, they boil the ingredients rather than carry out the extraction of the active principles with cold water. In these respects the method of preparation is similar to that of the Chazutas of Peru and notably different from that of the Tecunas and Javas of Brazil.

Approximate quantities of various ingredients used in the preparation of Curare by the Canelos Indians.

1. AS PREPARED IN THE VICINITY OF PACAYACU:

Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango") ..... 17.5 pounds
Stems of *Chondodendron tomentosum* ..... 11 pounds
Stems of *Chondodendron iquitanum* ("Nana Tonispa") ..... 11 pounds
Bark of stems of *Strychnos Mitscherlichii* ..... 1.5 pounds
Bark of *Ficus* sp. ..... 1 pound
Bark of roots of *Annona Ambotay* ..... 1 pound
Two small whole roots of *Lonchocarpus utilis* ..... 8 ounces

2. AS PREPARED BY A SECOND POISON-MAKER IN THE VICINITY OF PACAYACU:

Stems of *Sciadotenia toxifera*
Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")
Bark of roots of *Annona Ambotay*
Two small whole roots of *Lonchocarpus utilis*
Stems of *Chondodendron tomentosum*

3. AS PREPARED BY A THIRD POISON-MAKER IN THE VICINITY OF PACAYACU:

Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango") ..... 12 pounds
Stems of *Sciadotenia toxifera* ..... 11.5 pounds
Stems of *Chondodendron tomentosum* ..... 26 pounds
Bark of roots of *Strychnos Jobertiana* ..... 1 pound
Whole root of *Erythrochiton* sp. ..... 1 pound
Bark of roots of *Strychnos* sp. (*Gill 9*) ..... 1.5 pounds
Bark of roots of *Strychnos Peckii* ..... 12 ounces

Whole root of *Gill 24*	4 ounces
Bark of *Gill 25*	4 pounds
Bark of *Ficus* sp.	2 pounds

4. AS PREPARED IN THE VICINITY OF RIO CONAMBU:

Stems of *Chondodendron iquitanum* ("Yana Pala Ango")	6.5 pounds
Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")	11 pounds
Bark of roots of *Sciadotenia toxifera*	4 ounces
Stems of *Cissampelos pareira*	4.5 pounds
Bark of stems of *Strychnos toxifera*	2.5 pounds
Bark of stems of *Strychnos Peckii*	8 ounces
Bark of branches of *Gill 38*	1 pound
Bark of roots of *Strychnos* sp. (*Gill 9*)	2 ounces

SPECIMENS EXAMINED FROM THE TERRITORY INHABITED BY THE CANELOS INDIANS

MORACEAE

FICUS sp. The collection *Gill 7* suggests *F. paraensis* Miq. by the general shape and texture of its leaves, but has shorter petioles and lacks the prominent veinlet reticulation of the upper leaf surface which characterizes Miquel's species. *F. atrox* Mart. was reported (Buchner, Repert. Pharmacie **36:** 341. 1830; Lond. Jour. Bot. **6:** 550. 1847) as used in Curare, but that species has ovate leaves deeply cordate at the base and apparently is not closely related to ours. According to Gill, the present species is known to the Canelos as "Yana Ambi Caspi." Its bark is occasionally used as a secondary ingredient of Curare. It is probably the same species to which Karsten (3: 148) refers as "Yána hámbi cáspi."

MENISPERMACEAE

CHONDODENDRON IQUITANUM Diels. Of the plant components of Curare as prepared in different localities by the Canelos poison-makers, this species appears to be most commonly used as a main ingredient. All the preparations of the Canelos recorded by Gill include this plant, and in most cases it is used in quantities exceeding those of other ingredients. The macerated entire stems, including bark, are usually used. According to Gill, many poison-makers claim that this species alone makes a potent poison; he also states that it is common throughout the region.

We place in this species *Gill 6*, *12*, and *35*, collected under the names of "Nana Tonispa," "Tonispa Pala Ango," and "Yana Pala Ango" respectively. It appears from the collector's notes that the Canelos distinguish the three plants; although the specimens are sterile we place them in this species with confidence. These collections are the first record of the species from Ecuador, it being otherwise known only from the type locality in Peru near the mouth of Rio Santiago, above Pongo de Manseriche. The

species has recently been reported (4: 25) as used in Curare by certain Peruvian Indians. Karsten (3: 147), in listing the Quichua names of the plants used in Curare by the Canelos Indians, mentions "Pála huásca" as "a big flat liana, about 12 to 15 cm. in breadth. . . . Because of its flatness it is called 'the shovel-liana' (*pala* = 'shovel')." This seems to explain why two of the common names recorded by Gill for *C. iquitanum* (which, as all known species of *Chondodendron*, has a distinctly flat stem) make use of the word "pala." The word "tunishpa," according to Karsten, means "mixed" and is used to suggest the resemblance of one plant to another.

CHONDODENDRON TOMENTOSUM R. & P. The species has recently been reported (4: 18) as the main ingredient of the Curare of the Chazuta Indians of Peru. The present collection (*Gill 20*) is the first record of the species from Ecuador, although it has already been collected in Panama, Colombia, Peru, and Bolivia. The species is an important ingredient of the Curare of the Canelos, second only to *Chondodendron iquitanum*. It is evident from Gill's notes that certain poison-makers use even larger quantities of this plant than of *C. iquitanum*. The poison is made without it only in certain localities in the basin of Rio Conambu. The plant is known to the Canelos as "Tulumba Lamas Ango"; the entire stem, including bark and wood, is usually used by them.

Sciadotenia toxifera Krukoff & Smith, sp. nov. Frutex scandens; ramulis gracilibus teretibus cinereo-fuscis juventute minutissime pilosulis demum glabris; petiolis gracilibus striatis 3.5–6 cm. longis ut ramulis decidue cinereo-pilosulis; laminis maturitate subcoriaceis utrinque fusco-olivaceis late ovatis vel ovato-ellipticis, 14–22 cm. longis, 9–13 cm. latis, basi obtusis vel acutis vel cuneatis, apice abrupte cuspidatis vel caudato-acuminatis (acumine 5–25 mm. longo), margine leviter revolutis et saepe undulatis, utrinque glabris (vel juventute subtus ad nervos principales et secundarios parce puberulis mox glabris), 5 (vel obscure 7)-pli-nerviis, nervis primariis (superioribus 3–15 mm. supra basin orientibus) utrinque prominentibus, costa in laminae apicem terminante, nervis secundariis numerosis horizontalibus utrinque prominulis, venulis minute et conspicue reticulatis utrinque prominulis; inflorescentiis desideratis.

Type, *Gill 11*, collected Aug. 29, 1938, in dense forest near Pacayacu, in drainage of Rio Bobonaza and adjacent tributaries, basin of Rio Pastaza, Province of Napo-Pastaza, Ecuador, alt. 1000 m. *Gill 36*, from the Rio Conambu in the same general region, alt. 900 m., also represents the species.

These two specimens provide the first authentic evidence of the use of a member of this genus in Curare. From *S. similis* Moldenke, *S. Sprucei*

Diels, and *S. cayennensis* Benth., the new species is immediately distinguished by the comparatively large leaves, by the dense and fine veinlet reticulation which is conspicuously prominulous and discernible to the naked eye on both surfaces, and by the fact that the inner pair of principal nerves arises at a distance of 3–15 mm. above the base of the leaf blade. Its leaves are often faintly 7-pli-nerved as in *S. solimoesana* Moldenke, from which it is distinguished by the blades being cuneate to obtuse rather than truncate to subcordate at base, by the veinlets being conspicuously prominulous above rather than subimpressed, and by the fact that the blades are sparsely puberulent on the princpal nerves and secondaries beneath when young and at length glabrescent or glabrous, not obscurely but regularly appressed-puberulent on the lower surface. Although neither inflorescences nor fruits are available, we have no doubt that this is a new species, and it seems preferable to assign a name to it rather than to await more complete future collections.

The species appears to be a consistent and important component of the Curare of the Canelos. It is evident from Gill's notes that the poison is seldom prepared without it, and some poison-makers claim that a good Curare may be made from this plant alone. The entire stems, including bark and wood, are used by the Canelos. In the locality of Pacayacu it has been collected by Gill under the name of "Cuilin Ango," while in the basin of Rio Conambu he obtained it under the name of "Yana Ilucha." It is probably the same species to which Karsten (3: 147) refers as "Cüílin huásca" ("cüílin" = a bird of the toucan family), a small liana about 3 to 4 cm. in diameter.

CISSAMPELOS PAREIRA L. *Gill 20a* seems to agree well with the variety *typica* Diels. According to the collector, in certain localities in the basin of Rio Conambu the plant is used in place of *Chondodendron tomentosum* in Curare and is known to the natives under the same name, "Tulumba Lamas Ango."

A. C. Smith 3229, *Cissampelos ovalifolia* DC., was recently collected on savanna between the Takutu River and the Kanuku Mountains, British Guiana. The actual manufacture of Curare by the Macusi Indians stopped many years ago, but only within the last five years there was still living a medicine man who showed the principal plants which he used in "Urari" to Father H. C. Mather, S. J., of St. Ignatius Mission on the Takutu River. The present species was considered an important component. Possibly it is one of the unidentified plant-components of Macusi Curare listed by Richard Schomburgk (6: 353) under common names.

ANNONACEAE

ANNONA AMBOTAY Aubl. sens. lat. This species has already been reported as a component of the Curare of the Tecunas of Brazil (5: 405) and of the Chazuta Indians of Peru (4: 18). It is represented by *Gill 18;* the common name is reported as "Paguaga" or "Paguaga Caspi." The bark of roots is frequently used by the Canelos as a secondary ingredient of Curare. It is probably the same species as that referred to by Karsten (3: 148) as "Hambi pahuága."

GENUS UNCERTAIN. *Gill 15* is from a plant known to the Canelos as "Cara Caspi"; its bark is occasionally used as a secondary ingredient of Curare. This is possibly the same species to which Karsten (3: 148) refers as "Hámbi cára cáspi."

LEGUMINOSEAE

LONCHOCARPUS UTILIS A. C. Smith. This well-known fish-poison, represented by *Gill 53,* has already been reported as a component of the Curare of the Canelos by Karsten (3: 146), who refers to it as "Varváscu." Both Karsten and Gill report that the roots are used for this purpose.

RUTACEAE

ERYTHROCHITON sp. *Gill 21* is in fruit, and may be either *E. delitescens* Morton or *E. macropodum* Krause, or possibly an undescribed species. According to Gill the plant is known to the Canelos as "Soliman Caspi," and is occasionally used as a secondary ingredient in preparing the poison. A previous record of the use of Rutaceae in Curare is that of Richard Schomburgk (6: 353). He states that the Macusis use for this purpose the strongly bitter wood of "Manuca," "a tree of the family Xanthoxyleae."

LOGANIACEAE

STRYCHNOS TOXIFERA Rob. Schomb.; Benth. This species is well-known as the main ingredient of the Curare of the Macusi Indians of British Guiana, as was first ascertained by Robert Schomburgk in 1835 and verified by Richard Schomburgk in 1842. Spruce collected a specimen of it in the Cassiquiare region of Venezuela and reported on the label: "one of the species used by the Cunipusana Indians in the fabrication of Curare." Occasionally it is used in the Curare of the Tecunas of Brazil (5: 402, 406).

The present collection (*Gill 37*) is the first record of the species from Ecuador, extending its range approximately 600 miles to the west. The species thus is now known to occur from the Panama Canal Zone (*Standley*

27542, 28386, 31311, 41042; Pittier 2666; Kenoyer 479, 624; all deposited in the U. S. National Herbarium) to the mouth of Rio Embira (tributary of Rio Tarauaca) in the State of Amazonas, Brazil (*Krukoff 5081*), and from the Northwest District in British Guiana (*La Cruz 1358*) to the Pacayacu–Sarayacu region of the Province Napo-Pastaza in Ecuador. According to Gill the plant is known as "Julin Huasca" or "Julin Huasca Ango"; the bark of its stems is frequently used as a Curare ingredient by the Canelos.

STRYCHNOS GUIANENSIS (Aubl.) Baill. This species has a very extensive range, being fairly common in certain localities; it exhibits extraordinary variation in pubescence, leaf size and form, etc., often even on a single plant, and in addition it probably consists of a number of forms. When the American species of *Strychnos* are revised, many names will doubtless be reduced to synonymy under this binomial. It is not our present purpose to review the concept of this variable species, but we wish to mention certain authentic records of the use of *S. guianensis* and the related species (some of which may be conspecific with it) in Curare.

Schreber (7) reported the species, under the name *Toxicaria americana* Schreber, as one of the components of the Curare of certain tribes of Indians in Surinam.

Humboldt and Bonpland (2) mentioned "Curare" or "Bejuco de Mavacure" as one of the ingredients of the poison as prepared by Indians at Esmeralda on the upper Orinoco in Venezuela. This plant was formally described in 1825 and is the basis of *Strychnos Curare* (H. B. K.) Benth. (Jour. Linn. Soc. **1**: 108. 1856).

The type of *Strychnos depauperata* Baill. (Adansonia **12**: 372. 1879) is from the vicinity of Tonantins, Amazonas, Brazil; it was collected by Jobert and reported by him as one of the two species of *Strychnos* used by the "Kawichanes" Indians in preparing the poison.

The type of *Strychnos Crevauxiana* Baill. (Adansonia **12**: 377. 1879) is from the upper Paru, one of the northern tributaries of the Amazon; it was collected by Crevaux and reported by him as the main ingredient of the Curare of the Trios.

A. C. Smith 2836, a form of *Strychnos guianensis*, was recently collected in the basin of Shodikar Creek (Essequibo tributary) in British Guiana. The plant appears to be the most important component of Wai-wai Balauitú (arrow-poison). It is noteworthy that the Wai-wais, like the Trios, use chiefly the outer bark of roots.

The present collection of *S. guianensis* (*Gill 29*) is the first record from Ecuador, the species being well represented in herbaria from the Guianas, Venezuela, Brazil, and Peru. Doubtless it will also be found in Amazonian

Colombia. According to Gill the plant is usually referred to as "Payanche Chico"; its bark is occasionally used as one of the ingredients of Curare by the Canelos.

STRYCHNOS JOBERTIANA Baill. The type is from the vicinity of Tonantins, Amazonas, Brazil, collected by Jobert and reported by him as one of the two species of *Strychnos* used by the "Kawichanes" Indians in preparing the poison. It is also a component of the Curare of the Javas of Brazil and Peru (5: 407, 409). The plant was re-collected in 1936–37 in the Municipality of São Paulo de Olivença, Amazonas, Brazil (*Krukoff 7786, 7802*). The following specimens, all from the State of Amazonas, Brazil, probably represent a juvenile form of the species: *Krukoff 7990* from the immediate vicinity of Manaos, *Krukoff 7799* from the type locality, and *Krukoff 8848* from the basin of Creek Belem.

The present collections (*Gill 19, 74*) are the first record of the species for Ecuador, extending its range approximately 600 miles to the west. The species, which is obviously related to *Strychnos trichostyla* Ducke, doubtless occurs in Amazonian Colombia and Peru. According to Gill the plant is known as "Quilio Huasca"; its bark is used occasionally as one of the ingredients of Curare by the Canelos.

STRYCHNOS PECKII Rob. The present collection (*Gill 22*) appears to be the first authentic evidence of the use of the species in Curare. *Krukoff 7549, 7581, 7628–7632* inclusive, cited as *Strychnos* sp. in our earlier paper (5: 406) and reported as occasionally used in Curare by the Tecunas in Brazil, represent a closely allied plant which may prove conspecific with *Strychnos Peckii*. These specimens were studied by Sandwith and Krukoff in 1937 and were distributed as "*Strychnos* cf. *Peckii* Rob. var.? (group #1; material inadequate)."

The type of the species is from British Honduras. In South America it has been collected by Ducke in the State of Para, and is represented from the State of Amazonas, Brazil, by *Krukoff 8022* from the immediate vicinity of Manaos, and by *Krukoff 7778, 7780, 7789, 7832, 8973, 9054*, and *9108* from various localities in the Municipality São Paulo de Olivença. The present collection (*Gill 22*) is the first record of the species from Ecuador, extending its range approximately 600 miles to the west. The species obviously has a wide range and is to be expected in the countries between the known extremes.

According to Gill the plant is known as "Canon Huasca"; its bark is occasionally used as one of the ingredients of Curare by the Canelos. It is possible that the same Indian name was recorded by Karsten (3: 147) as "Cáñu huásca." However, he refers to a deep channel running along the

middle of the liana, from which it takes its name ("cáñu" = channel). This description hardly applies to *S. Peckii*.

STRYCHNOS MITSCHERLICHII Rich. Schomb. *Gill 5* appears to be the first authentic evidence of the use of this species in Curare. The plant is not used for that purpose by the Tecunas, although it is by far the most common species of *Strychnos* in their territory.

For a long time the species was considered as probably endemic to British Guiana. Recently it has been found in Surinam and in Brazil. Krukoff's collections from the State of Amazonas were identified by Sandwith and Krukoff and distributed as the following: *S. Mitscherlichii*, *S. Mitscherlichii* var. *pubescentior* Sandwith, *S. Mitscherlichii* var.? (group #18; material inadequate), *S. Mitscherlichii* var.? (group #41; material inadequate), and *S. Mitscherlichii* var.? (group #42; material inadequate). The collections are too numerous to cite here. The species appears to be as variable as *S. guianensis*.

The present collection (*Gill 5*) is the first record of the species from Ecuador. According to the collector it is known as "Caronsi Chaqui"; its bark is occasionally used as one of the ingredients of Curare by the Canelos.

STRYCHNOS sp. *Gill 9* is a sterile specimen in poor condition. We cannot match it satisfactorily with any species known to us, nor can we suggest its affinity. According to Gill the plant is known as "Payanche," and the bark of its roots is occasionally used as one of the ingredients of Curare by the Canelos. This is possibly the same species to which Karsten (3: 147) refers as "Payángshi."

RUBIACEAE

PSYCHOTRIA sp. *Gill 65* cannot be determined with certainty; it is probably an ally of *P. cuspidata* Bredem. The collector reports the common name, among the Canelos, as "Chirapa Caspi"; it is occasionally used as a secondary ingredient of their Curare.

FAMILY UNCERTAIN

Several specimens collected by Gill from species used in Curare by the Canelos are too incomplete to permit family identification. These are listed in the hope that eventually their identity will be determined.

Gill 24 is from a plant which the Canelos call "Seco Ango Callo" and which they sometimes use as a secondary ingredient of Curare.

Gill 25 represents a plant known to the Canelos as "Huayna Toa"; its bark is occasionally used as a secondary ingredient of their Curare.

Gill 38 is from a plant known to the Canelos as "Naucari Caspi"; occa-

sionally they use the bark of its stems and branches as a secondary ingredient of Curare.

SUMMARY

As a result of the study of botanical specimens collected by Mr. Gill, supplemented by his notes, we can draw the following conclusions.

1. The principal components of the Curare of the Canelos are invariably members of the Menispermaceae. In this respect their Curare resembles that of the Chazuta Indians of Peru, while it differs notably from the more eastern Curares such as those of the Javas, Tecunas, Trios, and Wai-wais of Brazil, of the Macusis of British Guiana and of certain tribes of the upper Orinoco basin in Venezuela. The main components of these Curares are species of *Strychnos*.

2. *Chondodendron iquitanum* appears to be the main ingredient of most preparations of the Canelos, while *C. tomentosum* and *Sciadotenia toxifera* are usually other important ingredients.

3. One or more species of *Strychnos* are often used in the Curare of the Canelos, *S. toxifera* being the most commonly used. However, it seems evident that the Canelos do not consider species of *Strychnos* to be essential ingredients, as the poison is often prepared without them.

4. A number of plants other than Menispermaceae and *Strychnos*, used as secondary ingredients by the Canelos, are of the same or related species which have already been reported as components of Curare of other South American Indians.

5. The absence of species of *Piper* in the Curare of the Canelos is conspicuous; in this respect it approaches the poison prepared by the Chazutas and differs from that prepared by the Tecunas, Javas, Trios, and Wai-wais.

THE NEW YORK BOTANICAL GARDEN

Literature cited

1. **Folkers, Karl.** 1938. Preliminary studies of the botanical components of Tecuna and Java curare. Jour. Am. Pharm. Assoc. **27**: 689–693.
2. **Humboldt, A. von and A. Bonpland.** 1807. Voyage aux régions équinoxiales du Nouveau-Continent (Relation histor. du voyage) **2**: 547–556.
3. **Karsten, Rafael.** 1935. The head-hunters of western Amazonas. Helsingfors.
4. **Krukoff, B. A. and H. N. Moldenke.** 1938. Studies of American Menispermaceae, with special reference to species used in preparation of arrow-poisons. Brittonia **3**: 1–74.
5. **Krukoff, B. A. and A. C. Smith.** 1937. Notes on the botanical components of curare. Bull. Torrey Club **64**: 401–409.
6. **Schomburgk, Richard.** 1922. Travels in British Guiana 1840–1844. Translated and edited by Walter E. Roth, vol. 1. Georgetown.
7. **Schreber, J. C. D. von.** 1783. Ueber das Pfeilgift der Amerikaner in Guiana, und die Gewächse aus denen es bereitet wird. Der Naturforscher **19**: 129–158.

The Morphology and Phylogenetic Position of the Genus Jouvea (Gramineae)[1]

PAUL WEATHERWAX

(WITH ELEVEN FIGURES)

On the Pacific coast of Mexico and Central America there are two grasses, constituting the genus *Jouvea*, which present certain unsolved problems of morphology and taxonomy. The two species, *J. straminea* Fourn. and *J. pilosa* (Presl.) Scribn., are apparently concise and at the same time sufficiently distinct from each other to conform with any ordinary concept of the species in general; but the correct position of the genus itself is not so well determined.

The staminate inflorescence is so similar to those of other grasses that it is easily understood. The pistillate inflorescence, however, shows no external resemblance to the staminate, and morphologically it seems to have no counterpart anywhere in the grass family. Different interpretations of it have been given, but no serious morphological study of it has ever been made. It was a statement of the need of such a study, in a comparatively recent taxonomic work (Hitchcock, 1930, p. 585) which first drew my attention to this genus and led me to make a side-trip from Guatemala City down to San José, in March, 1932, to secure specimens and see the plant in the field.

HISTORICAL

The genus *Jouvea*, established by Fournier in 1876, was based upon a pistillate plant of *J. straminea*, which he found in a collection made by Liebmann in Mexico several years previously. There is something of the ironical in Fournier's experience with this species. Having only the pistillate form and apparently misinterpreting that, he gave it a taxonomic position which has been difficult to maintain, and he drew from it a part of a generalization on monoecism and dioecism which the staminate form now completely refutes (Prat, 1933, p. 387). If Fournier had correctly interpreted the Liebmann collection, he might have avoided these errors, for it contained also staminate specimens of *Jouvea* (Scribner, 1896, p. 141).

[1] Contribution No. 77 from the Waterman Institute of Indiana University.

This is one of a series of studies on tropical American grasses, the collection of which was made possible by grants from the American Association for the Advancement of Science, the Society of the Sigma Xi, and the National Research Council and by aid of many kinds given by the United Fruit Company. Support for these studies has also been provided for many years by Indiana University through the Waterman Institute and the research facilities of the Graduate School.

Aside from its inclusion in taxonomic works, without additional information of a critical nature, we next meet *Jouvea* in the literature in 1890, when Vasey and Scribner separately report having found specimens in a collection made by E. Palmer in Lower California.[2] The plant which they describe, with good figures, is evidently what is now known as *J. pilosa*, but this name was not to be applied to it until later.

Vasey (1890) gives a good description of the plant and discusses the significance of the pistillate inflorescence. Not satisfied with Hackel's opinion that it should be placed in Fournier's genus *Jouvea*, he assigns it to a new genus and names the species *Rachidospermum mexicanum*. Vasey's difficulty was partly in the fact that he did not have access to Fournier's original description and partly in his not knowing that he was attempting to reconcile the characteristics of *J. pilosa* with a description of *J. straminea*.

Scribner (1890) more fortunately recognizes the plant as a species of *Jouvea* and tentatively assumes that it is *J. straminea*, although he admits that it does not agree with the description in all details. His figures, which are unmistakably of staminate and pistillate specimens of *J. pilosa*, are labeled "*Jouvea straminea*, Fourn.?".

In a second article (1896), Scribner corrects his error in identification and recognizes the two species, *J. pilosa* and *J. straminea*, essentially as we know them to-day.

The morphological findings of these investigators will be discussed in connection with the description and interpretation of the pistillate inflorescence.

MATERIAL

Jouvea pilosa proved to be an easy plant to find at San José; it formed almost a continuous colony along the top and seaward slope of the ridge of black sand on the two miles or more of beach examined. At first, *J. straminea* seemed not to be present, but, thanks to a few prominent staminate plants, it soon became evident that literally acres of the marshy flats on the landward side of the beach ridge were covered with it. The dull, bluish-green color and wiry habit of the plants had caused me to relegate them temporarily to some other family, such as the Juncaceae.

Aware of the species problem involved when two closely related plants occur together in this way, I spent some time looking for indications of hybridization but found none. In many places male plants of one species

[2] Note that this is Lower California, not California. As far as is known at present, *Jouvea* has not been found within the United States. Prat's statement (1933, p. 357) that it is found in California is probably due to the assumption that Lower California is a part of California.

were certainly close enough to females of the other for cross-pollination to occur; and the fully exposed stigmas, typical development of the anthers, and dioecious nature of both species indicate that wind pollination most certainly occurs.

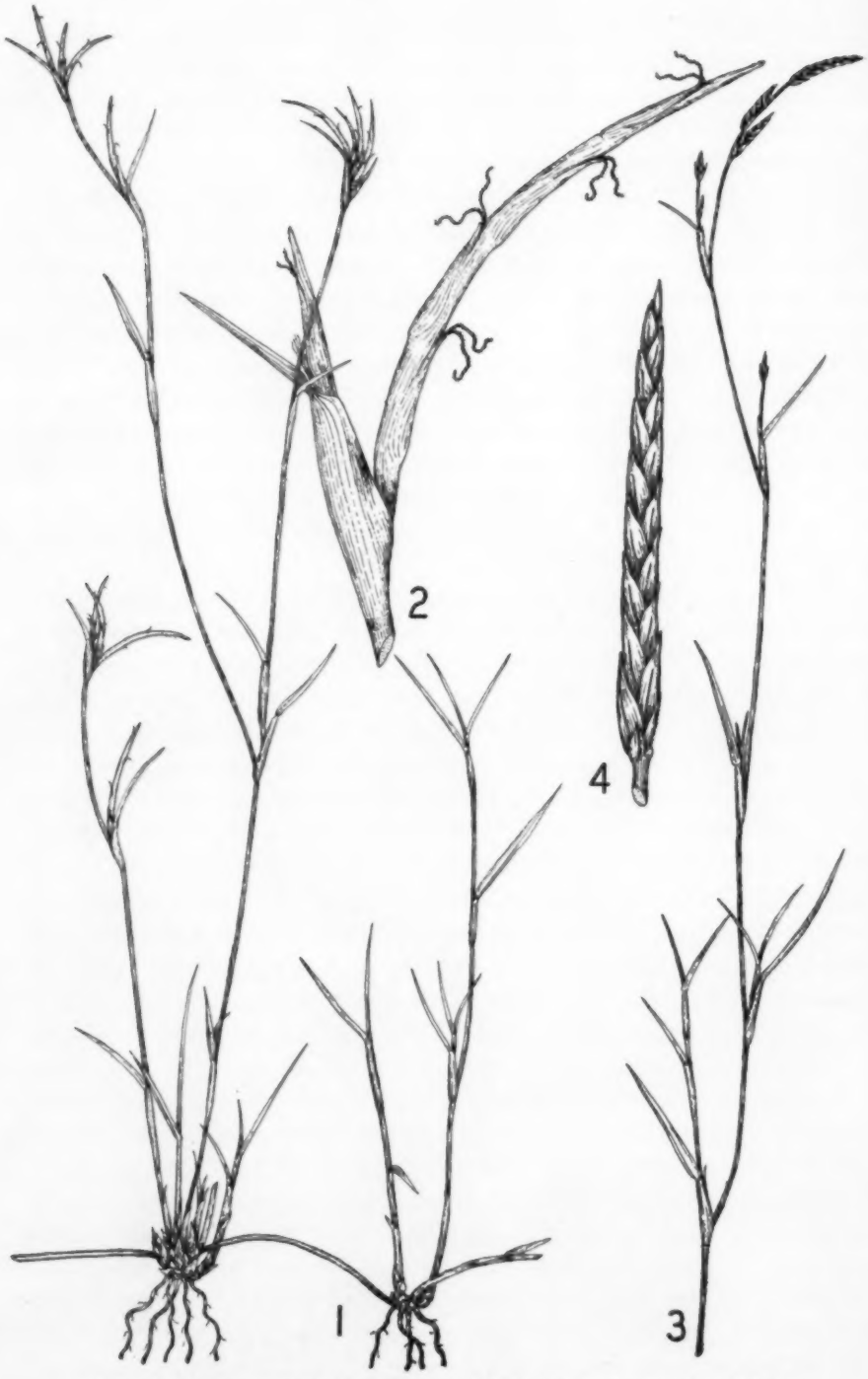
From the material collected it has been possible to make a very satisfactory study of most of the morphological features which seem to have any bearing on the phylogeny of the genus and the homologies of the pistillate inflorescence. Sufficient herbarium material has been available that an almost unlimited amount could be dissected and the range of variation of different parts studied. From collections preserved in formal-acetic-alcohol, good microtome sections have been made of stems, leaves, spikelets, and even entire fascicles of young pistillate inflorescences. Seeds of *J. pilosa* have also been germinated so that the structure of the seedling could be studied, but greenhouse conditions were apparently not favorable for the growth of seedling plants to maturity.

STAMINATE INFLORESCENCE

If all parts of these plants were as amenable to interpretation as are the staminate spikelets, the problem would be simple. As far as they alone are concerned, the resemblance to *Uniola*, *Distichlis*, *Lolium*, or *Agropyron* would suggest affinities with the Festuceae or the Hordeae, the final allocation depending upon characteristics outside the spikelet.

In *J. pilosa* (Fig. 6) some of the staminate spikelets are short and oblong, containing from 10 to 15 florets, while others are longer, linear in shape, and containing from 25 to 50 florets. These two types, although fairly distinct, seem to be due to environmental factors. At the time of year at which the collection was made (March) all of the long spikelets were old and weather-beaten, while the short ones were still alive, some even immature, but complete as to primordial development. The corresponding spikelets of *J. straminea* (Figs. 3, 4) are essentially like those of *J. pilosa* but smaller. They usually have from five to seven florets and seldom more than 15 or 20.

In both species the staminate spikelets are arranged in long-peduncled, definitely dorsiventral spikes, with the uppermost spikelet apparently terminal on the rachis. In *J. pilosa* the spikes are clustered in axillary fascicles, each of which consists of a short branching system, leafless except for prophylls, with the end of each ultimate branch elongating to form the spike. In *J. straminea* these axillary branches are more simple, each usually producing one, and seldom more than two or three spikes. The spikelets are acropetal in flowering, but any one inflorescence produced from an axillary branch is basipetal.



Figs. 1–4. *Jouvea straminea*. Figs. 1, 2. Pistillate plant and spikelet. Figs. 3, 4. Staminate plant and spikelet.

The staminate florets have the usual lemma and palea and a flower consisting of two lodicules and three stamens. There is no visible rudiment of a pistil and apparently not even a vascular rudiment leading to the position where a pistil would be expected.

PISTILLATE INFLORESCENCE

The ultimate unit of the pistillate inflorescence is a curved, thorn-like structure, in the sides of which the flowers are imbedded in two rows in alternate arrangement (Figs. 2, 10). In *J. pilosa* (Fig. 10) the number of

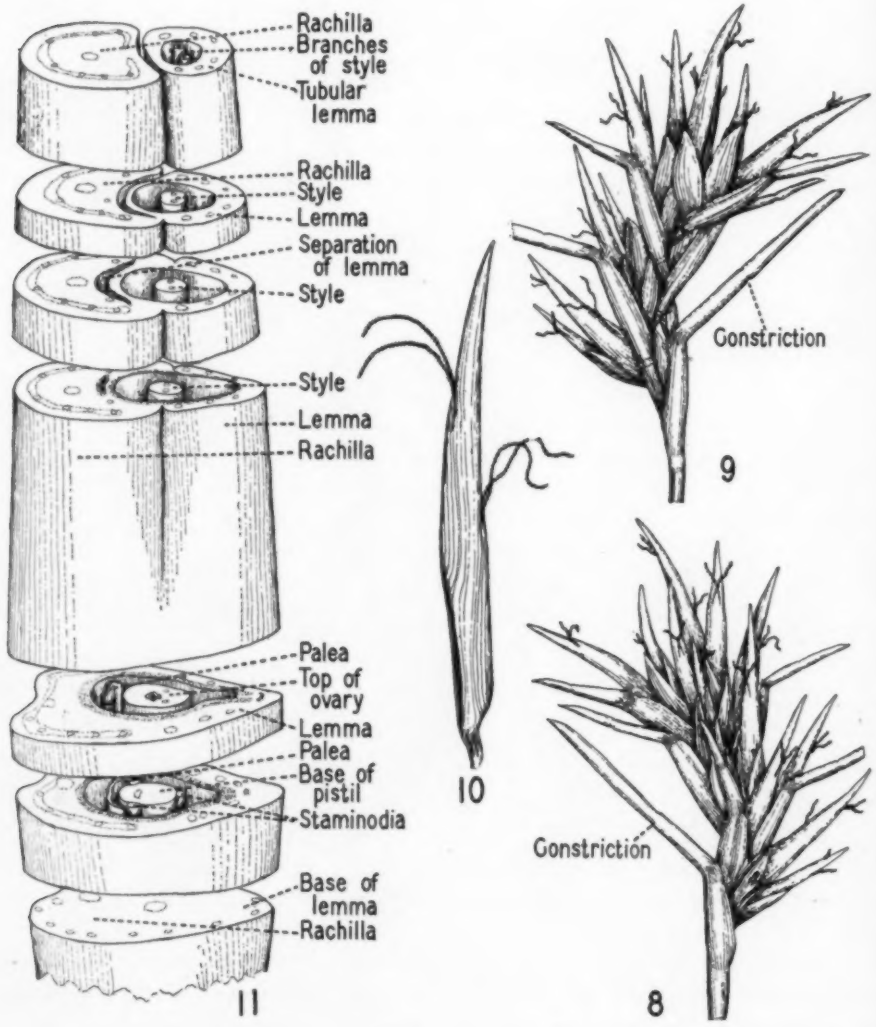
Figs. 5, 6. Pistillate and staminate plants of *Jouvea pilosa*. Fig. 7. Copy of Scribner's figure, showing a second flower (*J. straminea*).

flowers may be as low as two, with sometimes only the lower one functional; but in *J. straminea* (Fig. 2) there may be as many as four or five, with only the uppermost one rudimentary.

The morphological interpretation of this pistillate structure is the problem. Does it consist of a rachis with greatly reduced one-flowered spikelets imbedded in it, so that it resembles the *spike* of *Lepturus*, *Rottboellia*, *Tripsacum*, or *Stenotaphrum*, or is it an anomalous *spikelet* with the flowers imbedded in the thickened rachilla? Both views have been held, but no thorough morphological analysis has ever been made.

Fournier (1876, pp. 475–476) seems to have no other idea than that this structure is a spike, with the one-flowered spikelets imbedded in the

rachis. He describes the spikelets as having two glumes, with the inner separate from the rachis only at the top, and two small, narrow palets.[3]



Figs. 8–11. *Jouvea pilosa*. Figs. 8, 9. Ventral and dorsal views of a pistillate branch. Fig. 10. Pistillate spikelet. Fig. 11. Diagrammatic view, drawn to scale, of a pistillate spikelet sectioned at seven levels through one floret.

Vasey (1890) also raises the question of the morphology of the pistillate part of the plant. Without citing any real evidence, he agrees with

[3] "Glumae 2, exterior cartilaginea, straminea, interna hyalina, apice tantum a rachide distincta. Paleae duae, angustae, minores."

Fournier that it is a spike with the spikelets imbedded in the thickened rachis, each of the latter being reduced to a single pistil and possibly a lemma.

Scribner's interpretation (1890) of it as a spike agrees in most repects with the preceding, although he correctly points out that Fournier's description mentions some parts which cannot actually be found in the material. In a second article (1896) he gives, for the first time, serious consideration to the idea that the pistillate structure may be a spikelet, with the florets imbedded in a thickened rachilla, and that its resemblance to the spikes of *Lepturus* and *Monerma* may be only a simulation. But he makes one other interesting observation. In describing the pistillate "spikelet" he says (p. 143) that in many instances in *J. straminea* he found, above the palea of the ordinary floret, a second, imperfectly developed pistil enclosed in a membranous sac like that around the perfectly developed flower (Fig. 7). This would constitute almost positive evidence that the imbedded structures were spikelets rather than florets; and it is difficult to see why, in possession of a unique bit of evidence favoring one side of the question, he should conclude with exactly the opposite view. He clearly recognizes the significance of the point but apparently chooses to ignore it.

Hitchcock at one time (1913, pp. 190, 384) regards the structure as a spike; later (1930, p. 585) he calls it a spikelet but adds: "However, that which is called a spikelet may be a spike with 1 to 3 spikelets imbedded. Morphological research is needed here."

All evidences which I have been able to obtain from the material at hand lend support to the view that the pistillate structure in question is a spikelet, and future references to it, including the labels of the figures, will be made from this point of view. This does not entirely eliminate the possibility of some future observation which might change the picture. The evidence is mostly negative in nature. To call it a spike is to imply more deviation from the type of its staminate homologue than is necessary in view of what we know about it.

In some ten or twelve flowers of each species from which good series of sections have been obtained, there is perfect uniformity in all details which are regarded as significant; and these results have been substantiated by the dissection of probably 200 florets of each of the species from herbarium material.

The spikelet consists of a thick, spongy rachilla with the flowers deeply imbedded in its sides (Figs. 2, 10). The lowest flower of the spikelet seems to be, in all instances, the most advanced in development, and the uppermost is often imperfectly developed. The tip of the rachilla, prolonged beyond the uppermost floret, ends in a sharp point which becomes hard and thornlike at maturity.

The indurated lemma covers the cavity in which the flower is located and is adnate to the rachilla except at the top (Fig. 11). The nature of this adnation is not wholly clear, but it seems that the lemma is really a tubular sheath around the flower, and this tube is adnate to the rachilla for the greater part of its length. I know of no other grass in which the lemma is tubular, but there seems to be no reason why it might not be. It is generally regarded as the sheath of a leaf, and vegetative leaf sheaths are often tubular.

The flower is functionally pistillate, but short rudiments of the three stamens are regularly present in both species. The style is divided into two parts only in the upper, stigmatic portion, the greater part of which is exserted from the tubular opening of the lemma. No lodicules have been observed, and, if they were present, they certainly could not perform their usual function, on account of the peculiar form of the lemma. The palea is thin and membranous, and the two keels are usually evident; but there are no vascular bundles.

Fournier's statement that there are two glumes, two paleae, and two lodicules (squamulae) cannot be reconciled with these observations, but it is possible, in part, to explain his statement. Apparently having no idea but that what we call a spikelet was a spike, he expected to find two glumes and interpreted the outer part of the lemma as one and the inner part as the other. The palea sometimes splits when dry material is dissected, and it is possible that these two parts were regarded as the two separate bracts which he expected to find. Microtome sections are a most helpful safeguard in interpreting dissections of these structures.

It is more difficult to explain Scribner's observation of a second flower, in some cases, above the one ordinarily seen. His Figure *e*, Plate 266, copied here as Figure 7, is very convincing except for the fact that I have found nothing of the kind in any of the material which I have examined. It seems hardly possible that, in dissecting dry material, he could have broken off a fragment which would have been so deceptive as to have resulted in the figure which he gives. Granting that the material which I have examined, and which was collected in one locality, may not have shown the full range of variation of the parts in question, I am forced to regard his figure with some skepticism until I have seen an actual specimen which will substantiate its accuracy.

There is a further question as to why the finding of this second flower did not have more influence upon Scribner's interpretation of the pistillate inflorescence. A second flower in the position indicated would constitute most convincing evidence that the structure was a spike, but, even after discussing this point, he goes counter to prevailing opinion and concludes

that it is a spikelet. In view of all these uncertainties, we cannot give much weight to this report until the observation is repeated.

In the inflorescence the position of these pistillate units corresponds exactly with that of entire *spikes* in the staminate plants, but they may be interpreted as spikes which have contracted to the point where only the terminal spikelet remains. A careful search for remnants of lost spikelets, or for a spike composed of two or more spikelets not subtended by prophylls, might yield positive results.

TAXONOMIC POSITION

Although the early investigators placed *Jouvea* in the Hordeae, this way of disposing of it has not been very satisfactory. The staminate spikes are much like the inflorescences of *Agropyron* or *Lolium*, and the pistillate inflorescences resemble externally the spike of *Lepturus;* but even if we were to grant that the pistillate structure were a spike, which now seems improbable, there would still be a question as to whether *Lepturus* were closely enough related to *Lolium* and *Agropyron* to make their respective resemblances to the two sexes of *Jouvea* significant.

Prat (1933) has recently made a special study of *Jouvea* in developing and applying a new criterion for the division of the grasses into two subfamilies. He finds certain correlations which lead him to believe that the epidermal cells and the trichomes of the leaves may be used as a guide, the trichomes of the Pooideae being unicellular, while those of the Panicoideae consist of two or more cells. On this basis, he takes *Jouvea*, not only out of the Hordeae, but even out of the Pooideae, and places it in the Panicoideae.

His observation of the trichomes of *Jouvea*, particularly those of the ligule, is correct; they are usually composed of two or more cells. But the queer alignments which result from the application of his method to the entire grass family (Prat, 1933) engender a serious doubt as to the value of this criterion of classification. If we are to take *Jouvea* out of the Hordeae, we must certainly hope for a better alternative than to place it in the Panicoideae.

According to Schwendener's method (1890) of separating the two subfamilies, *Jouvea* would be placed in the Pooideae. Both Prat's figures and the sections which I have made of leaf blades show the mestome sheath which Schwendener designates as a characteristic of that sub-family.

A few other tests of relationship may be mentioned in passing, although they cannot be given much weight until their application to general problems of grass phylogeny is better known. No chromosome counts have been reported for either species of *Jouvea*. The absence of auricles on

the leaves and the profuse branching of the culms are hard to reconcile with the Hordeae. The few seedlings of *J. pilosa* which have been grown show a definitely elongated "mesocotyl," while the short type is regarded as more characteristic of the Hordeae. The taxonomic significance of this character is weakened, however, by the fact that at least one genus of Hordeae, namely, *Lolium*, has the elongated mesocotyl. The leaf blades of both species show, near the middle or toward the distal end, a peculiar constriction which is apparently due to some restraining effect as the leaf expands in the bud (Figs. 8, 9). This same characteristic is so well developed in *Agropyron* that it is regularly employed by farmers as an aid in identifying quack grass (*A. repens*). This same characteristic has, however, also been observed in at least two species of the bamboos.

These conflicting factors make it still difficult to dispose of *Jouvea* in any very satisfactory way. If we exclude for the moment Prat's classification, which seems to make matters worse rather than better, the possibilities are reduced to the Hordeae and the Festuceae; and the choice between these two will be difficult to make until we know better the meaning of some of the differences which now separate the tribes.

For the present I should prefer to be guided by the absence of auricles, the branched culm, the staminate inflorescence, and the similarity to *Distichlis* and *Uniola* and place *Jouvea* in the Festuceae, regarding the pistillate inflorescence as the result of one of those erratic ventures in evolution which have apparently occurred in so many genera of grasses.

SUMMARY

The morphological evidences available at present indicate that the characteristic thorn-like structure in which the pistillate flowers of *Jouvea* are borne is a spikelet rather than a spike.

Each pistillate flower is deeply imbedded in the rachilla and covered by a tubular lemma which is adnate to the rachilla for the greater part of its length.

Nothing comparable with the second flower, above the functional one, as reported by Scribner, has been found in a large amount of material investigated. It is concluded that any interpretation depending upon this point should await a repetition of his observation.

The pistillate flower has three rudimentary stamens but no lodicules; the staminate flower has two lodicules but no rudiment of a pistil. The staminate spikelet is much like that of *Distichlis* and presents no serious morphological problem.

Without an exhaustive study of the differences between the Hordeae and the Festuceae it would be difficult to decide between the two as to the

proper place for *Jouvea*, but the weight of evidence at present favors placing it in the latter.

INDIANA UNIVERSITY
DEPARTMENT OF BOTANY
BLOOMINGTON, INDIANA

Literature cited

Fournier, Eug. 1876. Sur les Graminées mexicaines à sexes séparés. Bull. Soc. Roy. Bot. Belgique. **15:** 439–476.

Hitchcock, A. S. 1913. Mexican grasses in the National Herbarium. Contrib. U. S. Nat. Herb. **17:** 181–389.

————. 1930. The grasses of Central America. Contrib. U. S. Nat. Herb. **24:** 557–762.

Prat, Henri. 1933. Remarques sur la position systématique du genre *Jouvea* Fourn. et sur les limites de la tribu Hordées. Bull. Soc. Bot. France. **80:** 357–367.

————. 1936. La systématique des Graminées. Ann. Sci. Nat. Bot. **18:** 165–258.

Schwendener, S. 1890. Die Mestomscheiden der Gramineenblätter. Sitzingsber. preuss. Akad. Wiss. **1890:** 405–426.

Scribner, F. L. 1890. New or little known grasses. II. Bull. Torrey Bot. Club. **17:** 225–234.

————. 1896. Grass notes. Bull. Torrey Bot. Club. **23:** 141–151.

Vasey, George. 1890. A new grass. Bot. Gaz. **15:** 106–110.

The Taxonomy and Ecology of Agropyron spicatum and A. inerme

REXFORD F. DAUBENMIRE

During the course of intensive field work on prairie types where bluebunch wheatgrass dominates, the writer has made many observations which do not support the current taxonomic concepts of this grass.

The type specimen of *Agropyron spicatum* (Pursh) Scribn. and Smith (described in 1814) has long awns which are well reflexed from the spike. In 1897 Scribner and Smith described an awnless form of the species, then known as *A. divergens* Nees., calling it variety *inerme* and distinguishing it from the species by the awnless character alone. In 1909 Rydberg elevated the variety to the species *A. inerme* (Scribn. and Smith) Rydb.

Repeated observations in the field reveal every degree of intergradation between these allegedly distinct grasses. From completely awnless lemmas (*A. inerme*) one finds awns of any length up to about 2 centimeters. Frequently the lower spikelets on the inflorescence are totally awnless while the upper ones have awns varying from barely perceptible to a centimeter or more in length. Also one finds every intergradation from erect to strongly divergent awns. Usually the shorter the awn, the greater the tendency to remain erect as the spikelet matures, but instances where the reverse is true are common. The relative length of awns, as well as the degree of bending is fairly uniform for the same plant, but is scarcely identical on any two specimens.

Since the only character which distinguishes the members of this completely intergrading series is the nature of the awn, the group could be split into as many species, varieties, or forms as there are variations in awns. Hitchcock (1935), following the type specimens, called all awnless forms *Agropyron inerme*, and all forms with long divergent awns *A. spicatum*, while the intergrades apparently were not known to exist, for such specimens can not be keyed out nor are they mentioned under either species description. Tidestrom (1925) maintained the same distinction as Hitchcock but remarked the complete intergradation of the two extremes, In a recent manual to the flora of this region (St. John, 1937), the dividing line between the two "species" is placed so as to lump awnless with erect awned species under *A. inerme*.

The present status is quite unsatisfactory since (1) all forms which are known are not taken into account, and (2) a *completely intergrading* series of plants is arbitrarily split into *species* on a *single* character.

The writer is of the opinion that if the group is to be split, only two forms can be distinguished: (1) inflorescences in which none of the lemmas are awned, and (2) inflorescences in which some or all of the lemmas are

awned. Since both the characters of length and degree of bending vary without consistent relation to each other, the second group of variants must either be lumped under the same name, or else a dozen or more arbitrarily distinguished forms must be set up. The latter treatment would be unacceptable to most botanists.

If the forms are to be separated as above into the only two categories which can always be distinguished, the question arises as to whether they should be given specific rank similar to the present status, or whether they should be designated as the two most recognizable forms of the same polymorphic species.

A very strong point in favor of lumping all forms into the same species, aside from the complete morphological intergradation, is a peculiar yet identical physiological trait possessed by all forms. Under drier climates or more xeric edaphic conditions, all of these forms assume the bunch habit, but under a more mesic climate and on favorable soils the plants are always sod-formers and fruit less prolifically. According to current taxonomic viewpoints, the sod and bunch habits are fundamental and fixed characters of the species in this genus, for they are invariably used in keys to separate the species. If these characteristics are so fundamental, we have further evidence that this entire series of intergrading forms should be considered the same species, since all of them change from the bunch to the sod habit under conditions of a more favorable waterbalance of the environment,—an ability which no other species of the genus appears to have. It is remarkable that this sod habit has been so completely overlooked by taxonomists, for it has twice been described by plant ecologists (Weaver, 1917; Shantz, 1924).

Because of the complete intergradation of the awn character which forms the sole morphological basis of distinction, and because of the identical and unusual response to environmental variation in which the fundamental growth form is altered, the writer recommends that (1) a single species name (*Agropyron spicatum* (Pursh) Scribn. & Smith) be applied to the entire group, (2) the description of this species be broadened as follows to include all the variations now known: Some or all of the lemmas awned, awns erect to strongly divergent, varying in length from very short up to 20 mm. or more; plants of either the sod or bunch habit, (3) if any variant in the group is to be given nomenclatorial recognition, a single variety, differing from the species only by the complete absence of awns, be designated as *Agropyron spicatum* var. *inerme* Heller (see Hitchcock, 1935, p. 773).

DEPARTMENT OF BOTANY
UNIVERSITY OF IDAHO
MOSCOW, IDAHO

Literature cited

Hitchcock, A. S. 1935. Manual of the grasses of the United States. U.S.D.A. Misc. Publ. 200. pp. 1040.

St. John, H. 1937. Flora of southeastern Washington and of adjacent Idaho. Lancaster Press. pp. 531.

Shantz, H. L. 1924. Grassland and desert shrub, in Atlas Amer. Agr. Part I., Sec. E. U.S.D.A. pp. 29.

Tidestrom, I. 1925. Flora of Utah and Nevada. Contrib. U. S. Nat. Herb. **25**: 1–665.

Weaver, J. E. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho., Univ. Nebr. Studies **17**: 1–133.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the index may be addressed to the Treasurer of the Torrey Club.

Allard, H. A. A yellow-rayed form of *Solidago bicolor* on Big Cobbler Mountain, Fauquier County, Virginia. Claytonia **5**: 28–30. Ja 1939.

Allen, C. K. Studies in the Lauraceae. II. Some critical and new species of *Cinnamomum* and *Neocinnamomum*. Jour. Arnold Arbor. **20**: 44–63. Ja 1939.

Allen, O. N. & Allen, E. K. Root nodule bacteria of some tropical leguminous plants: II. Cross-inoculation tests within the cowpea group. Soil Sci. **47**: 63–76. Ja 1939.

Allington, W. B. The separation of plant viruses by chemical means. Phytopathology **28**: 902–918. *f. 1–3.* D 1938.

Anderson, O. C. A cytological study of resistance of Viking currant to infection by *Cronartium ribicola*. Phytopathology **29**: 26–40. *f. 1, 2.* Ja 1939.

Avery, P. Cytogenetic evidences of *Nicotiana phylesis* in the alta-group. Univ. California Publ. Bot. **18**: 153–194. N 1938.

Babcock, E. B. & Stebbins, G. L. The American species of *Crepis*. Their interrelationships and distribution as affected by polyploidy and apomixis. Carnegie Inst. Publ. 504: 1–100. *pl. 1–3+f. 1–34.* D 1938.

Baehni, C. Les Celtis Sud-Américains. Candollea **7**: 189–214. 1936–38.

Baehni, C. & Macbride, J. F. *Basistemon*, genre de Bignoniacées. Candollea **7**: 185–188. *f. 1.* 1936–38.

Baehni, C. & Macbride, J. F. *Struthanthus* et *Phthirusa* envisagés comme congénériques. Candollea **7**: 287–290. 1936–38.

Baehni, C. & Macbride, J. F. Remarques sur les Cruciferae-Sisymbrieae. Candollea **7**: 291–296. 1936–38.

Bàez, J. R. Observaciones fitogeográficas sobre la Pampa occidental de la Provincia de Córdoba. Rev. Argentina Agron. **5**: 165–170. S 1938.

Barss, H. P. Danger in unguarded seed importation. Phytopathology **28**: 939. D 1938.

Bell, F. The ferns of Greene County, Pennsylvania. Castanea **4**: 5, 6. Ja 1939.

Berry, W. Branching of *Callixylon*. Am. Jour. Sci. **237**: 124–129. *pl. 1, 2.* F 1939.

Black, L. M. Properties of the potato yellow-dwarf virus. Phytopathology **28**: 863–874. *f. 1, 2.* D 1938.

Blodgett, F. M. The spread of apple mosaic. Phytopathology **28**: 937, 938. D 1938.

Boas, F. Sobre el efecto de algunos iones en los microorganismos vegetales. Lilloa **2**: 317–326. *f. 1, 2.* 1938.

Boas, F. El fenómeno geotrópico y la acción de la eosina sobre ráices y tallos de las plantas. Lilloa **2**: 327–331. *f. 1, 2.* 1938.

Bonner, J. & Erickson, J. The *Phycomyces* assay for thiamin (vitamin B_1): the method and its chemical specificity. Am. Jour. Bot. **25**: 685–692. *f. 1.* N 1938.

Brasfield, T. W. Tropical Dacrymycetaceae. Lloydia **1**: 153–160. *f. 1–25.* D 1938.

Brown, R. W. & Houldsworth, E. The fruit of *Trapa? microphylla* Lesquereux. Jour. Washington Acad. Sci. **29**: 36–39. *f. 1–9.* 15 Ja 1939.

Burkholder, W. H. A bacterial blight of stocks caused by *Phytomonas syringae*. Phytopathology **28**: 935, 936. D 1938.

Camp, W. H. Studies in the Ericales. LV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and adjacent regions. Bull. Torrey Club **66**: 7–28. Ja 1939.

[Carter, L. R.] Report of a plant hunt in Texas. Missouri Bot. Gard. Bull. **26**: 180–187. *pl. 27, 28.* D 1938.

Carlson, M. C. The formation of nodal adventitious roots in *Salix cordata*. Am. Jour. Bot. **25**: 721–725. *f. 1–8.* N 1938.

Castellanos, A. Algunos observaciones relativas a los bosques antartándicos. Lilloa **2**: 333–339. *pl. 1, 2.* 1938.

Chapman, V. J. Some algal complexities. Rhodora **41**: 19–28. Ja 1939.

Charles, D. R. & Smith, H. H. Distinguishing between two types of gene action in quantitative inheritance. Genetics **24**: 34–48. Ja 1939.

Charles, V. K. A new entomogenous fungus on the corn earworm, *Heliothis obsoleta*. Phytopathology **28**: 893–897. *f. 1–3.* N 1938.

Chucka, J. A. Magnesium studies with the potato. Am. Potato Jour. **15**: 301–312. N 1938.

Clark, C. F., Stevenson, F. J. & Schaal, L. A. The inheritance of scab resistance in certain crosses and selfed lines of potatoes. Phytopathology **28**: 878–890. *f. 1–3.* D 1938.

Clausen, R. T. Some plants of New York. Torreya **39**: 1–9. Ja–F 1939.

Clausen, R. T. & Wahl, H. A. Plants of central Pennsylvania. Rhodora **41**: 28–34. Ja 1939.

Clute, W. N. Meaning of plant names. LXXIV. The sumachs. Am. Bot. **44**: 60–67. Ap 1938; LXXV. The hollies. **44**: 98–102. Jl 1938; LXXVI. Bittersweets and burning-bushes. **44**: 143–148. O 1938; LXXVII. Soapberries and their allies. **45**: 8–14. Ja 1939.

Clute, W. N. The ceriman. Am. Bot. **45**: 3, 4. *illust.* Ja 1939.

Cochran, L. C. & Hutchins, L. M. Further studies on host relationships of peach mosaic in southern California. Phytopathology **28**: 890–892. *f. 1.* D 1938.

Constance, L. The genus *Eucrypta* Nutt. Lloydia **1**: 143–152. *map.* D 1938.

Constance, L. The genera of the tribe Hydrophylleae of the Hydrophyllaceae. Madroño **5**: 28–33. Ja 1939.

Conzatti, C. Flora taxonomica Mexicana. 1^1: 1–47. 1938; 2^2: 1–15. 1938; 1–32. 1938.

Craig, R. T. *Mammillaria inaiae* sp. nov. Jour. Cactus & Succ. Soc. Am. **10**: 111, 112. Ja 1939.

Cutak, L. The misunderstood Kalanchoids. Gard. Chron. **43**: 53, 54. F 1939.

Degener, O. Flora Hawaiiensis or the new illustrated flora of the Hawaiian Islands. **3**: *unnumbered pages and illust.* 1938.

Descole, H. R. & O'Donell, C. A. El *Crinodendron tucumanum* Lillo y su relación son las especies chilenas del género. Lilloa **2**: 341–352. *pl. 1–4.* 1938.

Diehl, W. W. Virginia records for three rarely known fungi. Claytonia **5**: 30–32. Ja 1939.

Diels, L. Botanical results of the Archbold expedition's New Guinea records of Annonaceae and Menispermaceae. Jour. Arnold Arbor. **20**: 73, 74. Ja 1939.

Diettert, R. A. The morphology of *Artemisia tridentata* Nutt. Lloydia **1**: 3–74. *pl. 1–20+f. 1–163.* D 1938.

Dittmer, H. J. A quantitative study of the subterranean members of three field grasses. Am. Jour. Bot. **25**: 654–657. N 1938.

Dix, W. L. *Botrychium multifidum* in Pennsylvania. Torreya **39**: 13. Ja–F 1939.

Dodge, B. O. The ascocarp and ascospore formation in *Stevensea Wrightii.* Mycologia **31**: 96–108. *f. 1, 2.* Ja–F 1939.

Dowding, E. S. & Orr, H. The dermatophyte *Microsporum lanosum*. Mycologia **31**: 76–92. *f. 1–29*. Ja–F 1939.

Drouet, F. The Brazilian Myxophyceae. II. Am. Jour. Bot. **25**: 657–666. N 1938.

Dunegan, J. C. Germination experiments with overwintered teliospores of *Tranzschelia pruni-spinosae*. Phytopathology **29**: 72–78. *f. 1*. Ja 1939.

Dyal, S. C. Additional notes on the Valerianellas of North America. Rhodora **40**: 465–467. D 1938.

Dykstra, T. P. A study of viruses infecting European and American varieties of the potato, *Solanum tuberosum*. Phytopathology **29**: 40–67. *f. 1–7*. Ja 1939.

Eaton, R. J. The persistence of *Opuntia humifusa* in Concord, Massachusetts. Rhodora **40**: 486, 487. D 1938.

Ellis, E. L. & Delbrück, M. The growth of bacteriophage. Jour. Gen. Physiol. **22**: 365–384. *f. 1–3*. 20 Ja 1939.

Epling, C. A note on the occurrence of *Salvia* in the new world. Madroño **5**: 34–37. *f. 1–4*. Ja 1939.

Epling, C. Two Mexican species of *Hyptis*. Madroño **5**: 15, 16. Ja 1939.

Epling, C. *Scylla, Charybdis* and *Darwin*. Am. Nat. **72**: 547–561. *pl. 1, 2*. N–D 1938.

Epling, C. A revision of *Salvia*: subgenus *Calosphace*. Repert. Spec. Nov. Beih. **110**[1]: 1–160. *pl. 1–16*+*map*. 1–16. 30 N 1938.

Evans, A. W. The cladoniae of New Jersey—supplement. Torreya **38**: 137–149. N–D 1938.

Faull, J. H. A review and extension of our knowledge of *Calyptospora Geoppertiana* Kuehn. Jour. Arnold Arbor. **20**: 104–113. Ja 1939.

Fogelberg, S. O. The cytology of *Cuscuta*. Bull. Torrey Club **65**: 631–645. *pl. 32*. D 1938.

Fosberg, F. R. Notes on plants of the Pacific Islands. I. Bull. Torrey Club **65**: 607–614. D 1938.

Fulford, M. The cladoniae of eastern Kentucky. Lloydia **1**: 161–167. D 1938.

Garren, K. H. Studies on *Polyporus abietinus*. II. The utilization of cellulose and lignin by the fungus. Phytopathology **28**: 875–878. D 1938.

Gemmell, A. R. The degeneration of Metropolitan bent. Phytopathology **29**: 95–102. *f. 1–4*. Ja 1939.

Goldsworthy, M. C. & Smith, M. A. An apple leafspot associated with *Fabraea maculata*. Phytopathology **28**: 938. D 1938.

Greathouse, G. A. & Watkins, G. M. Berbeine as a factor in the resistance of *Mahonia trifoliolata* and *M. Swaseyi* to *Phymatotrichum* root rot. Am. Jour. Bot. **25:** 743–748. *f. 1–10.* D 1938.

Greenleaf, W. H. Induction of polyploidy in *Nicotiana* by hetero-auxin treatment. Jour. Heredity **29:** 451–464. *f. 1–7.* D 1938.

Gruchey, J. H. B. de. A preliminary study of the larger aquatic plants of Oklahoma with special reference to their value in fish culture. Oklahoma Agr. & Mich. Coll. Agr. Exp. Sta. Tech. Bull. **4:** 1–31. *f. 1–68.* O 1938.

Hagelstein, R. Scientific survey of Porto Rico and the Virgin Islands—Diatomaceae. N. Y. Acad. Sci. & Virgin Island **8³:** 313–450. *pl. 3–9.* 19 Ja 1939.

Harlow, M. W. & Wise, L. E. Contributions to the chemistry of the plant cell wall. VIII. The cellulose in hair cap moss. Am. Jour. Bot. **25:** 760. D 1938.

Hastings, G. T. Roadside trees of southern California. Torreya **38:** 150–154. N–D 1938.

Henrici, A. T. Molds, yeasts, and Actinomycetes. *i–x.* 1–296. *f. 1–100.* John Wiley & Sons. 1930.

Hollinshead, M. H. Planting ferns for pleasure. Torreya **39:** 10–12. Ja–F 1939.

Howell, J. W. A fossil pollen study of Kokomo Bog, Howard County, Indiana. Butler Univ. Bot. Stud. **4:** 117–127. F 1938.

Hurd-Karrer, A. M. Relation of sulphate to selenium absorption by plants. Am. Jour. Bot. **25:** 666–675. *f. 1–3.* N 1938.

Jennison, H. M. *Trillium erectum* var. *Blandum*, var. nov. Rhodora **40:** 485, 486. *pl. 536.* D 1938.

Jones, G. N. A snyopsis of the North American species of *Sorbus*. Jour. Arnold Arbor. **20:** 1–43. *pl. 226, 227.* Ja 1939.

Jones, H. A. & Borthwick, H. A. Influence of photoperiod and other factors on the formation of flower primordia in the potato. Am. Potato Jour. **15:** 331–336. *f. 1.* D 1938.

Johann, H. Scolecospores in Diplodia zeae. Phytopathology **29:** 67–71. *f. 1–3.* Ja 1939.

Karling, J. S. Studies on *Rhizophidium*. II. *Rhizophidium laterale*. Bull. Torrey Club **65:** 615–624. *pl. 31.* D 1938.

Keck, D. D. Revision of *Horkelia* and *Ivesia*. Lloydia **1:** 75–142. *f. 1–9.* D 1938.

Key, E. B. Virginia wildflower sanctuaries. Claytonia **5:** 21–27. Ja 1939.

Kobuski, C. E. New and noteworthy species of Asiatic *Jasminum*. Jour. Arnold Arbor. **20**: 64–72. Ja 1939.

Kukenthal C. Vorarbeiten zu einer Monographie der Rhynchosporoideae. III. Repert. Spec. Nov. **44**: 161–195. S 1938.
Includes 2 new varieties of *Schoenus* from North America.

Larson R. H., Albert, A. R. & Walker, J. C. Soil reaction in relation to potato scab. Am. Potato Jour. **15**: 325–330. N 1938.

Latzina, E. Ensayo de dureza, compacidad y porosidad efectuados con maderas del páis. Lilloa **2**: 353–412. 1938.

Lindegren, C. C. & Lindegren, G. Non-random crossing over in the second chromosome of *Neurospora crassa*. Genetics **24**: 1–7. Ja 1939.

Lindquist, J. C. El nombre valido de *Agaricus iodoformicus*. Rev. Argentina Agron. **5**: 187, 188. *illust.* S 1938.

Lundell, C. L. Six new trees and shrubs from tropical North America. Phytologia **1**: 305–309. Ja 1939.

Mains, E. B. *Bitzea*, a new genus in the Pucciniaceae. Mycologia **31**: 33–42. Ja–F 1939.

Mains, E. B. The genus *Blastospora*. Am. Jour. Bot. **25**: 677–679. N 1938.

Mains, E. B. Studies in the Uredinales, the genus *Chaconia*. Bull. Torrey Club **65**: 625–629. *f. 1–6*. D 1938.

Marchionatto, J. B. El "corazon mohoso" de al manzana. Rev. Argentina Agron. **5**: 179–186. *pl. 9, 10+f. 1*. S 1938.

Martin, G. W. The morphology of the basidium. Am. Jour. Bot. **25**: 682–685. N 1938.

Maxon, W. R. & Morton, C. V. New ferns from Bolivia and Peru. Bull. Torrey Club **66**: 39–45. *f. 1*. Ja 1939.

McCubbin, W. A. Fungi and human affairs. *i–vii*. 1–111. *f. 1–48*. 1924.

McDougall, W. B. & Baggley, H. A. Plants of Yellowstone National Park. U. S. Dept. Interior Nat. Park Service 1–160. *f. 1–115*. 1936.

McMinn, H. E. Notes on the genus *Ceanothus* in California. Madrono **5**: 13–15. Ja 1939.

McRostie, G. P., Hopkins, J. W. & Grace, N. H. Effect of phytohormone dusts on growth and yield of winter wheat varieties. Canadian Jour. Res. **16**: 510–515. D 1938.

Meredith, W. O. S. & Anderson, J. A. Varietal differences in barleys and malts. IV. Commonly measured properties and their correlations with nitrogen and 1000-kernel weight. Canadian Jour. Res. **16**: 497–509. D 1938.

Merrill, E. D. & Perry, L. M. Additional notes on Chinese Myrtaceae. Jour. Arnold Arbor. **20**: 102, 103. Ja 1939.

Michener, H. D. The action of ethylene on plant growth. Am. Jour. Bot. **25**: 711–720. *f. 1.* N 1938.

Mills, W. R. The influence of maturity of potato varieties upon their susceptibility to late blight. Am. Potato Jour. **15**: 318–325. N 1938.

Moldenke, H. N. Additional notes on the Eriocaulaceae—I. Phytologia **1**: 309–336. Ja 1939.

Morton, C. V. On the genus *Cyclodium*. Bull. Torrey Club **66**: 47–52. Ja 1939.

Moxon, A. L., Olson, O. E., Searight, W. V. & Sandals, K. M. The stratigraphic distribution of selenium in the Cretaceous formations of South Dakota and the selenium content of some associated vegetation. Am. Jour. Bot. **25**: 749–809. *map.* D 1938.

Murrill, W. A. Mushrooms of Alachua County. Mimeo. Cont. Herb. Univ. Fla. Agr. Exp. Sta. Gainesville, Fla. 1–25. S 1938.

Murrill, W. A. Trees of Alachua County. Mimeo. Cont. Herb. Univ. Fla. Agr. Exp. Sta. Gainesville, Fla. 1–10. Ja 1939.

Murrill, W. A. Fungi of Alachua County. Mimeo. Cont. Herb. Univ. Fla. Agr. Exp. Sta. Gainesville, Fla. 1–16. 10 Au 1938.

Murrill, W. A. Additional Alachua Basidiomycetes. Mimeo. Cont. Herb. Univ. Fla. Agr. Exp. Sta. Gainesville, Fla. 1–7. F 1939.

Murrill, W. A. Additions to Florida fungi. I. Bull. Torrey Club **66**: 29–37. *f. 1–3.* Ja 1939.

Murrill, W. A. Three new boletes. Mycologia **31**: 110–112. Ja–F 1939.

Murrill, W. A. New Florida Polypores. Bull. Torrey Club **65**: 647–661. *f. 1–5.* D 1938.

Mutinelli, A. Ensayo cultural de un maní poco conocido en la Rep. Argentina. Rev. Argentina Agron. **5**: 171–178. *pl. 7, 8+f. 1.* S 1938.

Naylor, E. E. & Sperry, J. J. Vegetative reproduction in *Chlorophytum elatum*. Am. Jour. Bot. **25**: 695–699. *f. 1–16.* N 1938.

Oberle, G. D. A genetic study of variations in floral morphology and function in cultivated forms of vitis. N. Y. State Agr. Exp. Sta. Tech. Bull. 250: 3–63. O 1938.

Osborn, H. T. Studies on pea virus. I. Phytopathology **28**: 923–934. *f. 1.* D 1938.

Osterhout, W. J. V. Changes of apparent ionic mobilities in protoplasm. IV. Influence of guaiacol on the effects of sodium and potassium in *Nitella*. Jour. Gen. Physiol. **22**: 417–427. *f. 1–6*. 20 Ja 1939.

Osterhout, W. J. V. & Hill, S. E. Chemical restoration in *Nitella*. III. Effects of inorganic salts. Proc. Nat. Acad. Sci. **25**: 3–6. Ja 1939.

Otto, J. H. Forest succession in the southern limits of early Wisconsin glaciation as indicated by a pollen spectrum from Bacon's Swamp, Marion County, Indiana. Butler Univ. Bot. Stud. **4**: 93–116. D 1938.

Pady, S. M. Observations on the rate of growth of ascocarps of *Peziza domiciliana*. Mycologia **31**: 53–55. Ja–F 1939.

Peebles, R. H. A new Arizona species of *Echinocereus*. Am. Jour. Bot. **25**: 675–677. *f. 1*. N 1938.

Pennell, F. W. Botanical results of the Archbold expedition's new and noteworthy Papuan Scrophulariaceae. II. Jour. Arnold Arbor. **20**: 75–84. Ja 1939.

Pérez-Moreau, R. A. Revisión de las *Hydrocotyle* argentinas. Lilloa **2**: 413–463. *pl. 1–6*+*f. 1–15*. 1938.

Peto, F. H. Hybridization of *Triticum* and *Agropyron*. V. Doubling the chromosome number in *T. vulgare* and F_1 of *T. vulgare* X *A. glaucum* by temperature treatments. Canadian Jour. Res. **16**: 516–529. *pl. 1*. D 1938.

Pinchard, J. A. & Shaw, L. Downy mildew infection of flue-cured tobacco in the field. Phytopathology **29**: 79–83. *f. 1–4*. Ja 1939.

Porsild, A. E. Flora of Little Diomede Island in Bering Strait. Trans. Royal Soc. Canada **32**: 21–38. 1938.

Pratt, R. Influence of deuterium oxide on the growth of *Chlorella vulgaris*. Am. Jour. Bot. **25**: 699–701. *f. 1, 2*. N 1938.

Prescott, G. W. Objectionable algae and their control in lakes and reservoirs. Louisiana Municipal Rev. $1^{2,3}$: Jl–O 1938.

Prescott, G. W. Further notes on the desmids of Isle Royale, Michigan. The genus *Cosmarium*. Papers Michigan Acad. Sci. **23**: 203–213. *pl. 1–4*. Ap 1938.

Price, W. C. & Wyckoff, W. G. Ultracentrifugation of juices from plants affected by tobacco necrosis. Phytopathology **29**: 83–94. *f. 1–4*. Ja 1939.

Ray, W. W. Contribution to knowledge of the genus *Taphrina* in North America. Mycologia **31**: 56–75. *f. 1–23*. Ja–F 1939.

Ray, W. W. Overwintering of *Taphrina robinsoniana*. Phytopathology **28**: 919–922. *f. 1*. D 1938.

Read, C. B. Some Psilophytales from the Hamilton group in western New York. Bull. Torrey Club **65**: 599–606. *pl. 30.* D 1938.

Record, S. J. American woods of the family Loganiaceae. Trop. Woods **56**: 9–13. 1 D 1938.

Record, S. J. What is the scientific name for Greenheart? Trop. Woods **56**: 5, 6. 1 D 1938.

Rehder, A. New species, varieties and combinations from the collections of Arnold Arboretum. Jour. Arnold Arbor. **20**: 85–101. Ja 1939.

Rehder, A. Bibliographical note on "Ehrh. Plantag." Jour. Arnold Arbor. **20**: 137. Ja 1939.

Reid, M. E. The effect of light on the accumulation of ascorbic acid in young cowpea plants. Am. Jour. Bot. **25**: 701–711. *pl. 1. f. 1–6.* N 1938.

Richards, R. R. A pollen profile of Otterbein Bog, Warren County, Indiana. Butler Univ. Bot. Stud. **4**: 128–140. D 1938.

Riley, H. P. A character analysis of colonies of *Iris fulva*, *Iris hexagona* var. *giganticaerulea* and natural hybrids. Am. Jour. Bot. **25**: 727–738. *f. 1–3.* D 1938.

Robbins, W. J. & Schmidt, M. B. Vitamin B_6, a growth substance for excised tomato roots. Proc. Nat. Acad. Sci. **25**: 1–3. Ja 1939.

Roberts, E. A. & Reynolds, H. W. The role of plant life in the history of Dutchess County. 1–44. *f. 1–21.* 1938.

Rosen, H. R. & Weetman, L. M. The 1938 crown-rust epidemic of oats in Arkansas in relation to hybrids of Bon and Victoria. Phytopathology **28**: 898–901. *f. 1.* D 1938.

Seaver, F. J. Photographs and descriptions of cup-fungi—XXXI. *Mollisiella.* Mycologia **31**: 93–95. *f. 1.* Ja–F 1939.

Seeler, E. V. *Thyronectria denigrata* (Winter) Seaver, the cause of disease in *Gleditsia.* Jour. Arnold Arbor. **20**: 114, 115. Ja 1939.

Severin, H. H. P. & Freitag, J. H. Western celery mosaic. Hilgardia **11**: 495–547. *pl. 1–8+f. 1–9.* S 1938.

Shreve, F. Observations on the vegetation of Chihuahua. Madroño **5**: 1–13. *pl. 1–3+f. 1.* Ja 1939.

Skoog, F., Broyer, T. C. & Grossenbacher, K. A. Effects of auxin on rates, periodicity, and osmotic relations in exudation. Am. Jour. Bot. **25**: 749–759. *f. 1–7.* D 1938.

Smart, R. F. The reactions of myxomycetous swarm-cells to temperature. Am. Jour. Bot. **25**: 679–682. N 1938.

Smith, C. P. Species lupinorum. **1**: 1–16. Ap 1938; **2**: 17–32. My 1938; **3**: 33–48. Jl 1938; **4**: 49–64. Jl 1938; **5**: 65–80. Au 1938; **6**: 81–96. O 1938.

Smith, F. H. Reduction divisions in triploid *Impatiens*. Am. Jour. Bot. **25**: 651–654. *f. 1–12*. N 1938.

Spencer, E. Y. & McCalla, A. G. Fractional solubility of gluten in sodium salicylate solutions. Canadian Jour. Res. **16**: 483–496. *f. 1–3*. D 1938.

Spotts, A. M. The violets of Colorado. Madroño **5**: 16–27. Ja 1939.

Sprague, R. & Cooke, W. B. Some Fungi Imperfecti from the Pacific northwest. Mycologia **31**: 43–52. Ja–F 1939.

Stevenson, F. J. Starch content in potatoes. Am. Potato Jour. **15**: 356, 357. D 1938.

Steyermark, J. A. A tomentose form of *Cladrastis lutea*. Rhodora **40**: 487. D 1938.

Steyermark, J. A. *Coldenia nuttallii* in Missouri. Rhodora **40**: 487. D 1938.

Thimann, K. V. & Delisle, A. L. The vegetative propagation of difficult plants. Jour. Arnold Arbor. **20**: 116–136. *pl. 228–231*. Ja 1939.

Thompson, R. H. *Coronastrum:* a new genus of algae in the family Scenedesmaceae. Am. Jour. Bot. **25**: 692–694. *f. 1–10*. N 1938.

Tillson, A. H. & Bamford, R. The foral anatomy of the Aurantioideae. Am. Jour. Bot. **25**: 780–793. *f. 1–49*. D 1938.

Toth, S. J. The stimulating effects of silicates on plant yields in relation to anion displacement. Soil Sci. **47**: 123–139. *pl. 1*. F 1939.

Triana, J. Especies y variedades de las Cinchonas de la "Quinologia de Bogota" (conclusión). Rev. Acad. Colombiana **2**: 377–416. *pl. 19–31*. Au–O 1938.

Umbreit, W. W. The growth of Actinomycetes on different varities of potatoes. Am. Potato Jour. **15**: 349–355. *f. 1, 2*. D 1938.

Wadleigh, C. H. & Shive, J. W. A microchemical study of the effects of boron deficiency in cotton seedlings. Soil Sci. **47**: 33–36. Ja 1939.

Wall, M. E. The role of potassium in plants. I. Effect of varying amounts of potassium on nitrogenous, carbohydrate, and mineral metabolism in the tomato plant. Soil Sci. **47**: 143–161. F 1939.

DIRECTORY OF DEALERS

IN MATERIALS OF SCIENCE

The firms listed in this section represent reputable dealers in materials for the laboratory, library, greenhouse, field and garden.

Before you make your purchases consult these firms.

You are assured of courteous treatment and an ample discount.

Mention the BULLETIN

Second Printing, March, 1939

A TEACHING GUIDE TO THE TREES AND SHRUBS OF GREATER NEW YORK

VIII + 76 pp.—map

By

ARTHUR HARMOUNT GRAVES, Ph.D.

Curator of Public Instruction, Brooklyn Botanic Garden

and

HESTER M. RUSK, A.M.

Instructor, Brooklyn Botanic Garden

ATTENTION IS CALLED TO THE FOLLOWING FEATURES

1. *Both trees* and *shrubs* are included (270 species in all).
2. *Both winter* and *summer* characters are given, with keys based on appearance at those seasons.
3. *Commonly cultivated* trees and shrubs are included.
4. The *essential vegetative* characters are emphasized—features by which the species may be recognized at any time of the year.
5. Technical terms are for the most part avoided.
6. Locations in Greater New York are given where good specimens are available for study.
7. The book *fits the pocket* and is therefore handy for field use.
8. The book can be used to advantage for the Northeastern U.S. and adjacent Canada as well as for the New York City region.

Price $ .75. 10 copies for $7.00. Postpaid

Published by the authors:

Brooklyn Botanic Garden

1000 Washington Avenue, Brooklyn, New York